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PHYTOLOGIA

An international journal to expedite plant systematic, phytogeographical and ecological publication

Vol. 83 November 1997 No. 5

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Published by Michael J. Warnock
185 Westridge Drive Huntsville, Texas 77340 U.S.A.
PHYTOLOGIA is printed on acid free paper.

PHYTOLOGIA (ISSN 00319430) is published monthly with two volumes per year by Michael J. Warnock, 185 Westridge Drive, Huntsville, TX 77340. Second Class postage paid at Huntsville, TX. © 1996 by PHYTOLOGIA. Annual domestic individual subscription (12 issues): $40.00. Annual domestic institutional subscription (12 issues): $44.00. Foreign and/or airmail postage extra. Single copy sales: current issue and back issues volume 72 to present: $4.00; back issues (previous to volume 72): $3.00; add $.75 per copy postage and handling US [$1.50 per copy foreign]). Back issue sales by volume: $17.00 per volume 42-71 (not all available as complete volumes); $21.00 per volume 72-present; add $3.00 per volume postage US ($6.00 per volume foreign). POSTMASTER: Send address changes to Phytologia, 185 Westridge Drive, Huntsville, TX 77340-8916.

Phytologia (November 1997) 83(5):333-344.

AN INVENTORY OF PLANT SPECIES IN THE PARAMO OF CAJANUMA, PODOCARPUS NATIONAL PARK ,(ECUADOR)

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ABSTRACT

The results of a floristic inventory are presented for the Páramo of Cajanuma (3150-3385 m elevation), located in Podocarpus National Park, southern Ecuador. A total of 130 species, representing 81 genera and 50 families, are reported. Species composition is discussed in relation to environmental factors and regional-scale floristic patterns. Special emphasis is given to the occurrence of woody species.

KEY WORDS: páramo, floristics, Podocarpus National Park, Andes, Neotropics, Ecuador

INTRODUCTION

Neotropical montane regions are frequently covered with páramo vegetation between 3000 and 4700 m elevation. This ecosystem occurs discontinuously between Costa Rica and northern Perú in areas where annual precipitation is above 1500 mm and evenly distributed across the year (Lauer 1981; Luteyn 1992). Although páramo is usually dominated by herbaceous species, a zone of shrub páramo (*sensu* Cuatrecasas 1968) may occur between the grass páramo and timberline. In Ecuador, páramo covers less than 2% of the total area (Luteyn *et al.* 1992), but it may include more than 3300 vascular plant species (Luteyn, in press).

Despite both the high species richness and rates of environmental degradation that characterize Ecuador's upper montane zone (*e.g.*, Acosta-Solís 1984; Balslev 1988; Luteyn 1992), relatively few floristic inventories of páramo communities have been published for Ecuador (but see Løjtnant & Molau 1982; Cerón & Toasa 1994; Keating 1995). The floristic composition of montane communities in southern Ecuador differs substantially from those of adjacent regions (Jørgensen *et al.* 1995), but few páramo studies of any sort have been conducted there (but see Lægaard 1992; Keating 1995; Ramsay & Oxley 1996). In this article, I document a botanical inventory conducted in the Páramo of Cajanuma, located in northwestern Podocarpus National Park (Figure 1). A species list is provided (Appendix 1), and I briefly discuss species composition in relation to ecological factors and regional floristic patterns.

STUDY SITE AND METHODS

Located in the provinces of Loja and Zamora-Chinchipe, Podocarpus National Park is the only major protected area in the southern tip of Ecuador (Figure 1). It encompasses 146,280 ha of montane ecosystems, protecting the only remaining zone of intact forest in Loja Province. The northwestern section of the park is located immediately to the southeast of Loja, the only large city in the region.

The terrain of northwestern Podocarpus National Park is dominated by low, rugged mountains of orogenic origin. Fieldwork was conducted near the Cordillera Oriental de Los Andes, a high ridge that generally runs north-south between 2900 and 3424 m elevation. Numerous steep ridges adjoin the Cordillera Oriental, connecting it to deep valleys located to the east and west. Soils are classified as either vertisols or inceptisols (White & Maldonado 1991).

This study was conducted above the Cajanuma Park Station (2850 m), where plant species diversity is exceptionally high even by Ecuadorian standards (see Bøgh 1992; Madsen & Øllgaard 1994). Montane forests extend up to approximately 3100 m, above which point the vegetation is characterized by a heterogeneous mixture of timberline forest and páramo communities. The annual rainfall above 2800 m is between 2000 and 4000 mm (Apolo 1984). In the páramo, diurnal temperature typically varies between 3° and 10° C, and winds often exceed 100 kph (Keating 1995).

The study site was located at 4° 09′ S, 79° 10′ W on a ridge extending to the east of the Cordillera Oriental (Figure 1). The ridge is 60 to 100 m wide, and is flanked by ravines to the north and south. Between the Cordillera Oriental and the timberline, the ridge measures nearly 350 m in length. Unlike most páramos located north of the park, this site has not experienced intense anthropogenic disturbances in the recent past. Grazing does not occur near the study site, and the vegetation near Cajanuma has not burned since November, 1985.

From the top of the ridge (3385 m) down to 3335 m, the site is covered with grass páramo and patches of shrub-dominated vegetation between 5 and 15 m in diameter. Continuous shrub páramo occurs between 3335 and 3150 m, where the treeline occurs. Between September, 1991 and July, 1992, plant collections were made between the top of the ridge and 3250 m. Below this point, the ridge is covered with a complex shrub páramo/timberline ecotone; a study of this vegetation is still in progress. Plant community patterns and vegetation structure of Cajanuma have been analyzed by Keating (1995 and ms). This article lists all of the species that occurred in plots utilized for this study, as well as ones that were found outside the plots. Plant specimens were deposited primarily in the herbarium at the Pontificia Universidad

Católica del Ecuador (Quito), and duplicates were sent to the Herbario Nacional del Ecuador (Quito) and the Universidad Nacional de Loja.

RESULTS AND DISCUSSION

A total of 50 families, 81 genera, and 130 plant species were collected in the Páramo of Cajanuma (Appendix 1). Sixty-six species (51%) are woody, whereas 64 (49%) are herbaceous. Taxonomically, 3 (2.3%) species are bryophytes, 13 (10%) are pteridophytes, and 114 (88%) are angiosperms. In terms of species richness, the most important families are Asteraceae (18), Ericaceae (14), and Melastomataceae (10). These three families tend to be among the most species-rich families in many Andean sites above 3000 m (see Gentry 1995). In contrast, 27 families are represented at Cajanuma by only one species.

In part because Cajanuma is located at a relatively low elevation, the grass páramo differs substantially from others sampled in northern South America (*e.g.*, Cleef 1981; Miller & Silander 1991; Hofstede 1995). Although grasses dominate most of the area above 3335 m elevation, only three members of Poaceae were collected, none of which are bunch grasses. *Chusquea loxensis* L.G. Clark is abundant throughout the site, although *Calamagrostis macrophylla* (Pilger) Pilger appears to be the most abundant grass species. Since many other grass taxa are known from adjacent areas (L. Clark & S. Lægaard, pers. comm.), it is very likely that some taxa were inadvertently missed.

Secondly, unlike páramos sampled at higher elevations, the Cajanuma páramo contains relatively few species of either the rosette or cushion life forms. Although four members of the Bromeliaceae, as well as *Valeriana convallarioides* (Schmale) B.B. Larsen, are found here, other rosette species found frequently at higher elevations in Colombia (*e.g.*, Cleef 1981) and Venezuela (*e.g.*, Pérez 1987) are absent at Cajanuma. Many species exhibiting this life form are adapted to sub-freezing soil temperatures (Pérez 1987), which do not characterize the Cordillera Oriental. Moreover, of the cushion plant taxa known to occur in the páramos north of Loja Province, only *Eriocaulon* spp. were collected at this site.

Finally, the Cajanuma grass páramo is atypical due to the richness of woody species (n=36), as well as the abundance of woody individuals. Not only are patches of tall (1-2 m) shrubs found in the upper páramo, but nearly all of the grass-dominated sites contain some woody individuals. *Arcytophyllum setosum* (R. & P.) Schlecht., *Disterigma empetrifolium* (H.B.K.) Drude, *Gynoxys miniphylla* Cuatrec., *Miconia latifolia* (D. Don) Naud., and *Valeriana microphylla* H.B.K. are most abundant (Keating 1995), and at least ten other shrub species are common. Most woody species in the grass páramo were also seen in the shrub páramo, but the following woody species were restricted to the grass páramo: *Disterigma codonanthum* H.B.K., *Gaultheria amoena* A.C. Smith, *Miconia bullata* (Turcz.) Triana, *Miconia rotundifolia* (D. Don) Naud., and *Pentacalia myrsinites* (Turcz.) Cuatrec. Given that many relatively undisturbed sections of the Cordillera Oriental are covered with tall shrubs, fire may play an important role in maintaining this community (*e.g.*, Keating 1997).

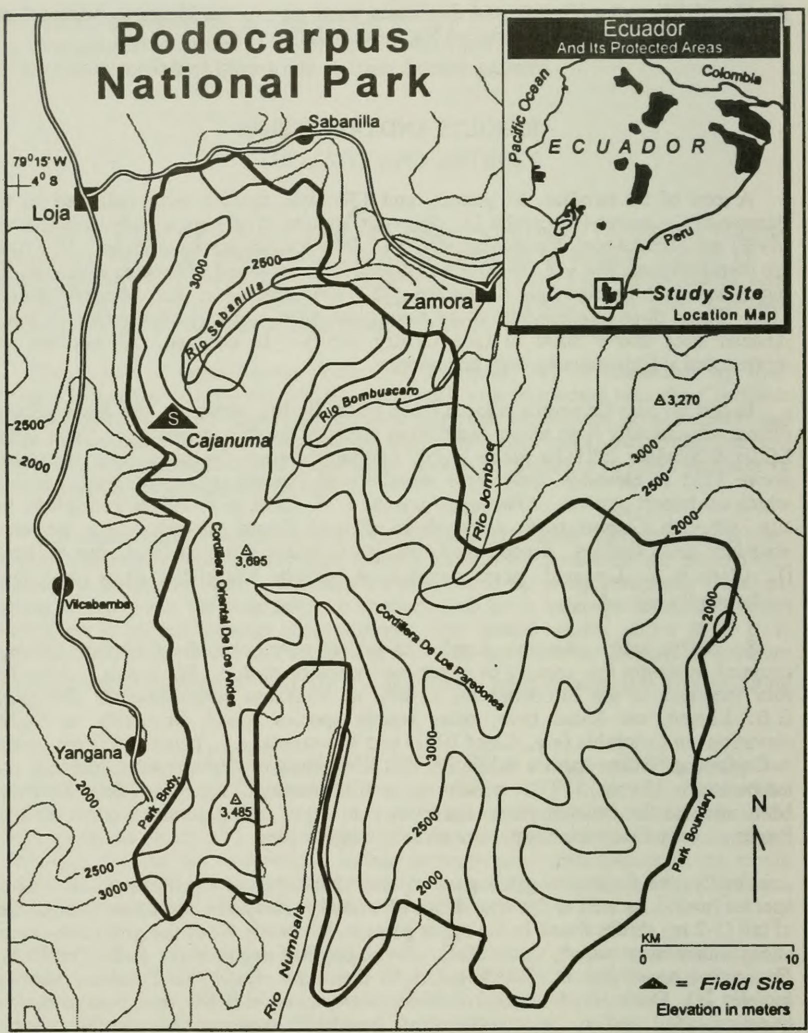

Figure 1. Map of Podocarpus National Park

Within the zone of continuous shrub páramo (< 3335 m), 61 woody species and 43 herbaceous species were collected. Although the majority of the woody species also occur above 3335 m, 23 were restricted to the lower shrub páramo (< 3320 m). Some of these species are probably uncommon in other Ecuadorian páramos, but it is difficult at this point to determine how rare these woody taxa are at the regional scale (see discussion below).

The vast majority of the 43 herbaceous species occurring in this community were also present in the grass páramo. Only four herbaceous species were unique to this community: *Baccharis huaracajensis* Hieron., *Greigia* or *Puya* sp., *Lophosoria quadripinnata* (Gmelin) C. Chr., and *Peperomia galioides* H.B.K. The most abundant herbaceous species in this community is *Tillandsia orbicularis* L.B. Sm., a rosette species of the Bromeliaceae. Whereas most *Tillandsia* species above the Cajanuma Park Station are arboreal epiphytes (e.g., Bøgh 1992), this species attains 100% coverage in much of the shrub páramo.

Although shrub páramo is often found above timberline in tropical montane regions (*e.g.*, Cleef 1981; Smith & Young 1987; Frantzen & Bouman 1989), most recent páramo studies conducted in Ecuador pertain only to grass-dominated communities. Given that many high-elevation shrub species may be eliminated by frequent fires (*e.g.*, Williamson *et al.* 1986; Horn 1989; Keating 1995), this community is severely threatened by the increasing frequency of anthropogenic disturbances above 3000 m (*e.g.*, Lægaard 1992; Keating 1997). Extensive areas of shrub páramo have been eliminated throughout the Andes, and scientists will need to study this community more intensively to ensure that it receives greater protection in the future.

According to Luteyn (in press), the páramos of Podocarpus National Park not only exhibit unusually high species diversity, but differ significantly in floristic composition from those páramos located in more northern regions. It is difficult, however, to make quantitative comparisons between the site described above and those sampled in more northern sites. First, previous studies differ markedly with respect to both the sampling scheme utilized and the area surveyed. Second, while botanists have collected specimens in the Loja Province for more than five decades (*e.g.*, Espinosa 1948), both the park and southwestern Ecuador in general remain undercollected (Jørgensen *et al.* 1995).

Although the majority of the 50 families found at Cajanuma are common throughout the high Andes, many of the species may be uncommon in other Andean páramo sites. As this study was conducted, many additional species were observed in other páramo communities along the Cordillera Oriental. More extensive investigations will be necessary to provide accurate estimates of the total species diversity and level of endemism that characterize páramos within the park. However, recent studies (Jørgensen & Ulloa Ulloa 1995; Young & Reynel 1997) have suggested that montane ecosystems of both southern Ecuador and northern Perú contain many endemic plant species. Because Podocarpus National Park includes thousands of hectares of relatively undisturbed páramo, it merits far more attention by páramo specialists than it has been accorded previously.

ACKNOWLEDGMENTS

This project was funded by the John T. and Catherine D. MacArthur Foundation, the Fulbright Commission of Ecuador, and the Ibero-Latin American Studies Center at the University of Colorado. I thank the following individuals for identifying plant specimens: Bruce Allen, Lynn Clark, Peter M. Jørgensen, Simon Lægaard, Blanca León, James L. Luteyn, Harry Luther, Bolívar Merino, Benjamin Øllgaard, Harold Robinson, Katya Romoleroux, Neil Snow, and Kenneth R. Young. Finally, I thank Drs. Bradley Bennett and Neil Snow for providing critiques of an earlier draft of this manuscript, realizing that any shortcomings of the article are the fault of the author alone.

REFERENCES CITED

Acosta-Solís, M. 1984. *Los Páramos Andinos del Ecuador.* Publicaciónes Científicas MAS, Quito, Ecuador.

Apolo, W. 1984. *Plan de Manejo Para el Parque Nacional Podocarpus.* Ministerio de Agricultura y Ganadería, Quito, Ecuador.

Balslev, H. 1988. Distribution patterns of Ecuadorian plant species. Taxon 37:567-577.

Bøgh, A. 1992. Composition and distribution of the vascular epiphyte flora of an Ecuadorian montane rain forest. Selbyana 13:25-34.

Cerón, C.E. & G. Toasa. 1994. Diversidad de la vegetación en el Volcán Rumiñahui, Pichincha, Ecuador. Rev. Geográfica 34:21-41 (Ecuador).

Cleef, A.M. 1981. The Vegetation of the Páramos of the Colombian Cordillera Oriental. Dissertationes Botanicae 61:1-320, J. Cramer, Vaduz, Liechtenstein.

Cuatrecasas, J. 1968. Páramo vegetation and its lifeforms. Pp. 163-186, *In* C. Troll (ed.). *Geo-ecology of the Mountainous Regions of the Tropical Americas.* Colloquium Geographicum 9, Bonn, Germany.

Espinosa, R. 1948. *Estudios Botánicos en el Sur del Ecuador,* Vol. 1. Universidad Nacional de Loja, Ecuador.

Frantzen, N. & F. Bouman. 1989. Dispersal and growth form patterns of some zonal páramo vegetation types. Acta Bot. Neerl. 38:449-465.

Gentry, A.H. 1995. Patterns of diversity of floristic composition in neotropical montane forests. Pp. 103-126, *In* S.P. Churchill, H. Balslev, E. Forero, & J.L. Luteyn (eds.). *Biodiversity and Conservation of Neotropical Montane Forests.* New York Botanical Garden, Bronx, New York.

Hofstede, R.G.M. 1995. Effects of burning and grazing on a Colombian páramo ecosystem. Ph.D. Dissertation, University of Amsterdam, The Netherlands.

Horn, S.P. 1989. Postfire vegetation development in the Costa Rican páramos. Madroño 36:93-114.

Jørgensen, P.M. & C. Ulloa Ulloa. 1995. Plant Diversity and Geography of Southwestern Ecuador. Final report on field activities. National Geographic Society, Grant No. 5181-94.

Jørgensen, P.M., C. Ulloa Ulloa, J.E. Madsen, & R. Valencia. 1995. A floristic analysis of the high Andes of Ecuador. Pp. 221-237, *In* S.P. Churchill, H. Balslev, E. Forero, & J.L. Luteyn (eds.). *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, Bronx, New York.

Keating, P.L. 1995. Disturbance Regimes and Regeneration Dynamics of Upper Montane Forests and Páramos in the Southern Ecuadorian Andes. Unpublished Ph.D. Dissertation, Department of Geography, University of Colorado, Boulder, Colorado.

Keating, P.L. 1997. Mapping vegetation and anthropogenic disturbances in southern Ecuador with remote sensing techniques: implications for park management. Yearbook of the Conference of Latin Americanist Geographers 23:77-90.

Keating, P.L. MS. Changes in páramo vegetation along an elevational gradient in southern Ecuador. For publication in J. Torrey Bot. Soc.

Lægaard, S. 1992. Influence of fire in the grass páramo vegetation of Ecuador. Pp. 151-170, *In* H. Balslev & J.L. Luteyn (eds.). *Páramo: An Andean Ecosystem under Human Influence*. Academic Press, London, Great Britain.

Lauer, W. 1981. Ecoclimatological conditions of the páramo belt in the tropical high mountains. Mountain Res. Dev. 1:209-221.

Løjtnant, B. & U. Molau. 1982. Analysis of a virgin páramo plant community on Volcán Sumaco, Ecuador. Nordic J. Bot. 2:567-574.

Luteyn, J.L. 1992. Páramos: why study them? Pp. 1-15, *In* H. Balslev & J.L. Luteyn (eds.). *Páramo: An Andean Ecosystem Under Human Influence*. Academic Press, London, Great Britain.

Luteyn, J.L. In press. Páramos: a checklist of plant diversity, geographical distribution, and botanical literature. Memoirs of the New York Botanical Garden, Bronx, New York.

Luteyn, J.L., A.M. Cleef, & O. Rangel Ch. 1992. Plant diversity in páramo: towards a checklist of páramo plants and a generic flora. Pp. 71-84, *In* H. Balslev & J.L. Luteyn (eds.). *Páramo: An Andean Ecosystem Under Human Influence*. Academic Press, London, Great Britain.

Madsen, J.E. & B. Øllgaard. 1994. Floristic composition, structure and dynamics of an upper montane rain forest in southern Ecuador. Nordic J. Bot. 14:403-423.

Miller, G.A. & J.A. Silander. 1991. Control of the distribution of giant rosette species of *Puya* (Bromeliaceae) in the Ecuadorian páramos. Biotropica 23:124-133.

Pérez, F.L. 1987. Soil moisture and the upper altitudinal limit of giant páramo rosettes. J. Biogeogr. 14:173-186.

Ramsay, P.M. & E.R.B. Oxley. 1996. Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Vegetatio 124:129-144.

Smith, A.P. & T.P. Young. 1987. Tropical alpine plant ecology. Annual Rev. Ecol. Syst. 18:137-158.

White, S. & F. Maldonado. 1991. The use and conservation of natural resources in the Andes of southern Ecuador. Mountain Res. Dev. 11:37-55.

Williamson, G.B., G.E. Schatz, A. Avlarado, C.S. Redhead, A.C. Stam, & R.W. Sterner. 1986. Effects of repeated fires on tropical páramo vegetation. Trop. Ecol. 27:62-69.

Young, K.R. & C. Reynel. 1997. Huancabamba Region. Peru and Ecuador. Pp. 465-469, *In* S.D. Davis, V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, & A.C. Hamilton (eds.). *Centres of Plant Diversity: A Guide and Strategy for* *their Conservation*, Vol. 3: The Americas. The World Wide Fund for Nature and The World Conservation Union, London, Great Britain.

APPENDIX I

Plant taxa that occur in the Páramo of Cajanuma (3250-3385 m), Podocarpus National Park. A total of 50 families, 81 genera, and 130 species are included. Numbers in parentheses indicate the author's collection number(s).

Family, species, and voucher number	Habit
I. Bryophytes	
BARTRAMIACEAE	
Breutelia chrysea (C. Mull.) Jaeg. (509)	herb
DICRANACEAE	
Campylopus jamesonii (Hook.) Jaeg. (507)	herb
RHACOCARPACEAE	
Rhacocarpus purpurascens (Brid.) Par. (507a)	herb
II. Pteridophytes	
ADIANTACEAE	
Jamesonia cf. *imbricata* (Sw.) Hook. & Grev. (191)	herb
BLECHNACEAE	
Blechnum cf. *auratum* (Fée) *comb. ined.* (275)	herb
GLEICHENIACEAE	
Gleichenia revoluta H.B.K. (265)	herb
HYMENOPHYLLACEAE	
Hymenophyllum sp. (277)	herb
ISOETACEAE	
Isoetes sp. (278)	herb
LOPHOSORIACEAE	
Lophosoria quadripinnata (Gmelin) C. Chr. (253)	herb
LYCOPODIACEAE	
Huperzia brevifolia (Grev. & Hook.) Holub (188)	herb
Huperzia cf. *kuesteri* (Nessel) Øllgaard (114, 180)	herb

Lycopodium clavatum L. (152)	herb
Lycopodium magellanicum (Palisot) Sw. (235)	herb
Lycopodium vestitum Poir. *in* Lam. (163)	herb
POLYPODIACEAE	
Polypodium aff. *punctulatum* Hook. (269)	herb
THELYPTERIDACEAE	
Thelypteris (*Amauropelta*) sp. (284)	herb

III. Angiosperms

APIACEAE	
Niphogeton dissecta Benth. (167)	herb
AQUIFOLIACEAE	
Ilex sp. (172, 239)	tree
ASTERACEAE	
Ageratina cutervensis (Hieron.) K.M. King & H. Rob. (403)	scandent forb
Baccharis huaracajensis Hieron. (200, 405, 512)	scandent forb
Diplostephium asplundii Cuatrec. (179, 406)	shrub
Diplostephium espinosae Cuatrec. (413)	shrub
Diplostephium hartwegii Hieron. (110, 132, 193)	shrub
Diplostephium sp. (139, 403)	shrub
Eupatorium sp. (137)	scandent forb
Gynoxys cuichensis Cuatrec. (129, 162)	shrub
Gynoxys miniphylla Cuatrec. (122, 169)	shrub
Gynoxys sp. (502)	tree
Hieracium cf. *frigidum* Wedd. (264)	herb
Mikania brachyphylla Hieron. (418)	herbaceous vine
Oritrophium peruvianum (Lam.) Cuatrec. (208)	herb
Pentacalia myrsinites (Turcz.) Cuatrec. (401)	shrub
Pentacalia oronocensis (DC.) Cuatrec. (203)	shrub
Senecio pimpinellifolia H.B.K. (190)	herb
Senecio tephrosioides Turcz. (198)	herb
unknown #1 (210)	herb
BERBERIDACEAE	
Berberis sp. (263)	shrub
BORAGINACEAE	
Moritzia lindenii (DC.) Gurke *ex* Benth. (22)	herb
BRASSICACEAE	
Cardamine cf. *ovata* Benth. (1, 42, 161)	herb
BROMELIACEAE	
Greigia sp. (257)	herb
Greigia or *Puya* sp. (255)	herb

Puya maculata L.B. Sm. (256)	herb
Tillandsia orbicularis L.B. Sm. (204)	herb
CAMPANULACEAE	
Centropogon steyermarkii Jepp. (135)	shrub
CARYOPHYLLACEAE	
Stellaria recurvata H.B.K. (136)	scandent forb
CLETHRACEAE	
Clethra fimbriata H.B.K. (151)	tree
Clethra ovalifolia Turcz. (112, 209)	tree
CLUSIACEAE	
Hypericum aciculare Kunth (105)	shrub
Hypericum decandrum Turcz. (194)	shrub
Hypericum lancioides Cuatrec. (126, 202)	shrub
CUNONIACEAE	
Weinmannia elliptica H.B.K. (119)	tree
Weinmannia cf. *fagaroides* H.B.K. (185)	shrub
Weinmannia glabra L.*f.* (157)	tree
Weinmannia rollottii Killip (28, 138)	tree
CYPERACEAE	
Rhynchospora sp. (508)	herb
ERICACEAE	
Disterigma acuminatum (H.B.K.) Nied. (164)	shrub
Disterigma alaternoides (H.B.K.) Nied. (156)	shrub
Disterigma codonanthum H.B.K. (117)	shrub
Disterigma empetrifolium (H.B.K.) Drude (133)	shrub
Gaultheria amoena A.C. Smith (276)	subshrub
Gaultheria erecta Vent. (4, 248)	shrub
Gaultheria megalodonta A.C. Smith (116)	shrub
Gaultheria reticulata H.B.K. (5, 244)	shrub
Gaultheria strigosa Benth. var. *strigosa* (3, 168)	shrub
Gaultheria sp. (270)	shrub
Macleania rupestris (H.B.K.) A.C. Smith (108)	shrub
Pernettya prostrata (Cav.) D.C. (6, 234)	shrub
Themistoclesia epiphytica A.C. Smith (21, 184)	shrub
Vaccinium floribundum H.B.K. (25, 251)	shrub
ERIOCAULACEAE	
Eriocaulon microcephalum H.B.K. (9)	herb
Eriocaulon sp. (175)	herb
GENTIANACEAE	
Halenia cf. *asclepiadea* (H.B.K.) G. Don (51, 196)	herb

GERANIACEAE	
Geranium mollendinense Kunth (7, 8, 102, 206)	herb
Geranium sibbaldioides Benth. (30, 205)	herb
GROSSULARIACEAE	
Escallonia myrtilloides L.*f.* (27)	shrub
Ribes hirtum H.B.K. (183)	tree
HALORAGACEAE	
Gunnera magellenica Lam. (33, 207)	herb
IRIDACEAE	
Sisyrinchium cf. *chilense* Hook. (32)	herb
LILIACEAE	
Bomarea cf. *densifolia* Vargas (103, 189)	herbaceous vine
Bomarea cf. *setacea* (R. & P.) Herb. (246)	herbaceous vine
MELASTOMATACEAE	
Brachyotum andreanum Cogn. (111)	tree
Meriana (Centronia) sanguinea Wurd. (45, 166)	tree
Miconia bullata (Turcz.) Triana (24, 115)	tree
Miconia cladonia Gleason (201)	tree
Miconia dodsonii Wurd. (177)	shrub
Miconia latifolia (D. Don) Naud. (107, 211)	tree
Miconia ligustrina (Sm.) Triana (287)	shrub
Miconia rotundifolia (D. Don) Naud. (120)	scandent shrub
Miconia salicifolia (Bonpl. *ex* Naud.) Naud. (109, 121)	tree
Miconia vaccinioides (Bonpl.) Naud. (195)	shrub
MYRSINACEAE	
Cybianthus marginatus (Benth.) Pipoly (267)	shrub
Myrsine dependens (R. & P.) Spreng. (266)	shrub
Myrsine sp. (280)	shrub
ONAGRACEAE	
Fuchsia loxensis H.B.K. (41)	scandent forb
ORCHIDACEAE	
Epidendrum sp. (268)	herb
Gomphichis cf. *valida* Rchb.*f.* (2, 165)	herb
OXALIDACEAE	
Oxalis cf. *lotoides* H.B.K. (47, 101)	scandent forb
Oxalis sp. (503)	herb
PIPERACEAE	
Peperomia galioides H.B.K. (245)	scandent forb
POACEAE	
Calamagrostis macrophylla (Pilger) Pilger (504)	herb

Chusquea loxensis L.G. Clark (505)	herb
Neurolepis asymmetrica L.G. Clark *ined.* (506)	herb
POLYGALACEAE	
Monnina cf. *revoluta* H.B.K. (124, 134)	shrub
POLYGONACEAE	
Muehlenbeckia tamnifolia (Kunth) Meissner (46, 118)	herbaceous vine
Rumex tolimensis Wedd. (279)	herb
ROSACEAE	
Hesperomeles heterophylla (R. & P.) Hook. (23)	shrub
Lachemilla cf. *nivalis* (Kunth) Rothm. (128, 199)	herb
Rubus acanthophyllos Focke (262)	scandent shrub
Rubus coriaceus Poir. (261)	scandent forb
Rubus loxensis Benth. (100, 187, 260)	scandent forb
RUBIACEAE	
Arcytophyllum capitatum (Benth.) K. Schum. (247)	shrub
Arcytophyllum setosum (R. & P.) Schlecht. (106, 181)	shrub
Nertera granadensis (Mutis *ex* L.*f.*) Druce (280)	herb
Relbunium hypocarpium (L.) Hemsl. (281)	herb
SMILACACEAE	
Smilax sp. (285)	herbaceous vine
SCROPHULARIACEAE	
Bartsia sp. (282)	herb
Calceolaria comosa Pennell (237)	shrub
Calceolaria oxyphylla Molau (31, 104, 130, 170)	tree
SOLANACEAE	
Unknown sp. 1 (43, 501)	treelet
Unknown sp. 2 (44)	treelet
Unknown sp. 3 (283)	treelet
SYMPLOCACEAE	
Symplocos clethrifolia Ståhl (174)	tree
Symplocos cf. *quitensis* Brand (160)	tree
Symplocos sp. 1 (286)	shrub
Symplocos sp. 2 (192)	shrub
VALERIANACEAE	
Valeriana convallarioides (Schmale) B.B. Larsen (178)	herb
Valeriana microphylla H.B.K. (113, 123, 171)	shrub
Valeriana plantaginea H.B.K. (131, 182)	herb
Valeriana sp. (173)	shrub
XYRIDACEAE	
Xyris subulata R. & P. (29)	herb

Phytologia (November 1997) 83(5):345-365.

ELYMUS STEBBINSII: TAXONOMY, NOMENCLATURE, AND DISTRIBUTION

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ABSTRACT

Elymus stebbinsii was originally named *Agropyron parishii* by Scribner & Smith, who recognized two varieties in it, *A. parishii* var. *parishii* and *A. parishii* var. *laeve*. Discovery that the holotype of var. *laeve* belongs in *E. trachycaulus* raised the question of whether there is a valid taxon corresponding to the description, but not the type, of var. *laeve*. Examination of specimens from several Californian herbaria, combined with phenetic analyses of morphological data, supports Scribner & Smith's recognition of a long-awned taxon within *E. stebbinsii* for which the name ***E. stebbinsii*** subsp. ***septentrionalis*** is proposed. This subspecies grows in the western Sierra Nevada and southern Cascade Mountains, whereas subsp. *stebbinsii* grows near the coast of northern California and in the Transverse Ranges. Herbarium records indicate that subsp. *septentrionalis* is the more abundant of the two taxa. The study also revealed that plants of *E. glaucus* may have anthers as long as 4.6 mm, a considerable increase over the previously reported upper limit of 3 mm. A key to the Californian species of *Elymus* is presented.

KEY WORDS: *Agropyron parishii, Agropyron parishii* var. *laeve, Elymus stebbinsii*, California, North America, taxonomy, nomenclature, Hordeeae, Triticeae, Poaceae

NOMENCLATURAL HISTORY

The basionym of *Elymus stebbinsii* Gould is *Agropyron parishii* Scribner & J.G. Sm., a species the authors (Scribner & Smith 1897) described as differing from other species then included in *Agropyron* by its pubescent culm nodes and widely spaced, long-glumed spikelets. The species description was followed by the description of var. *laeve*: "[having] the habit of the species, but the culm nodes and leaf sheaths glabrous; awns as long or longer than the flowering glumes. Type in the Gray Herbarium No. 414, Dr. Edward Palmer, collected at Talleys [misread as Fowleys by

Scribner & Smith], Cuiamaca [= Cuyamaca] Mountains, in the southern part of San Diego County, Cal., 1875". Table 1 summarizes the subsequent nomenclatural history of the two taxa.

Hitchcock (1912) raised var. *laeve* to a species as *Agropyron laeve*, but subsequently accepted Scribner & Smith's treatment of the two taxa (Hitchcock 1935, 1951), as did Munz (1959). Abrams (1940) treated both taxa as species. Gould (1947) was the first taxonomist to place the two varieties in *Elymus* L., but he also placed them in different species. He named transferred *Agropyron parishii* as *Elymus stebbinsii*, the combination *Elymus parishii* having been used earlier for another taxon (Hall 1902), but placed *A. parishii* var. *laeve* in *E. pauciflorus* (Schwein.) Gould as subsp. *laevis* (Scribner & J.G. Sm.) Gould. At the time, Gould thought that *Elymus pauciflorus* was the correct name for what had, until then, been known as *Agropyron trachycaulum* (Link) Malte, but Lamarck (1791) had already used it for another species. Shinners (1954) corrected Gould's oversight, publishing the combination *E. trachycaulus* (Link) Gould *ex* Shinners for *A. trachycaulum*, but did not publish a combination for *A. parishii* var. *laeve*. Thus, *A. parishii* var. *laeve* was left with no valid name in *Elymus*.

Gould gave no reason for changing the species to which var. *laeve* belonged, but it may have been as a result of examining the holotype. As Michael Curto pointed out (pers. comm., 1992), the holotype undoubtedly belongs in *Elymus trachycaulus*, having anthers about 2 mm long, whereas *Agropyron parishii* has anthers 3-6 mm long in addition to distant spikelets. The long awns of the holotype of var. *laeve* place it in *E. trachycaulus* subsp. *subsecundus* (Link) A. Löve & D. Löve.

Hoover (1966) agreed with Scribner & Smith that their *Agropyron parishii* included both unawned and awned plants, but did not consider that they merited separate recognition. He agreed with Gould, however, in placing the species in *Elymus*. Because Hoover combined *A. parishii* var. *laeve* with *A. laeve* var. *laeve* in a single species, he had to use *E. laevis* Hoover as its name, Hitchcock's (1912) publication of *A. laeve* giving that epithet priority over *stebbinsii* at the species level.

THE PROBLEM

The discovery that the holotype of *Agropyron parishii* var. *laeve* belongs in *Elymus trachycaulus* raised the question as to whether there is a long-awned variant of *A. parishii* that merits taxonomic recognition or whether all such plants belong to other taxa, the most likely candidates being *E. glaucus* or *E. trachycaulus* subsp. *subsecundus*.

Because UTC [herbarium codes from Holmgren *et al.* (1990)] has no specimens of *Agropyron parishii*, I borrowed specimens identified as *A. parishii, A. parishii* var. *laeve, Elymus stebbinsii*, or *E. laevis* from AHUC, CAS, CHSC, DAV, DS, JEPS, POM, RSA, and UC. I already had the holotype of *A. parishii* var. *parishii* on loan from US. Initial review of the specimens indicated that the problem was not simple. Many of the specimens borrowed belonged to *E. glaucus* or *E. trachycaulus*, but identifying them on the basis of existing keys (including Barkworth 1993) proved frustrating.

Both *Elymus glaucus* and *E. trachycaulus* have been described as variable (Snyder 1950; Dremann 1995; Barkworth 1996), but there are few details about their variability in the literature. *Elymus glaucus* supposedly differs from both *E. trachycaulus* and *E. stebbinsii* having two spikelets per node, but plants with some or all of their spikes having one spikelet per node are not uncommon. It usually has more lax leaves, longer anthers, and glume veins that are more evenly scabridulous than *E. trachycaulus*, but the distinction between the two is not easy, particularly when working with herbarium specimens. It has been thought to differ from *E. stebbinsii* in having shorter anthers (1.5-3.0 mm vs. 3-6 mm; Barkworth 1993), but applying this range to identification of the loaned specimens made it evident that the upper limit needed revising.

Elymus trachycaulus supposedly differs from *Agropyron parishii* in its more imbricate spikelets and shorter anthers (0.8-2.5 mm vs. 3-6 mm). There are specimens of *E. trachycaulus* with distant spikelets, but the anther distinction is usually sufficiently consistent to be a reliable means of distinguishing between the two taxa if anthers are present. If they are not, the two taxa are hard to distinguish using existing keys.

After several unsatisfactory attempts to identify the specimens, I decided to conduct a morphometric study of the specimens. In addition to determining whether *Elymus stebbinsii* had infraspecific taxa that merited recognition, I hoped to find additional characters that, either singly or in combination with others, would make it easier to distinguish between *E. stebbinsii, E. glaucus*, and *E. trachycaulus*.

MATERIALS AND METHODS

The total number of specimens employed in this study was 168. Among them were the holotype and one isotype of *Agropyron parishii* var. *parishii* (US 556669 and DS 79635, respectively). I had examined the holotype of *A. parishii* var. *laeve* previously and, after convincing myself that it was *Elymus trachycaulus*, had returned it to GH. There were no isotypes of var. *laeve* among the specimens borrowed. I also requested a loan of the taxa from SD, but all the specimens that had at one time been placed in *A. parishii* or *E. stebbinsii* had since been annotated as belonging to other taxa, primarily *E. trachycaulus*. These were made available to me shortly after I had completed the major part of this study. I examined each specimen but found none that belonged in *E. stebbinsii*; consequently, they are not included in the data presented here.

Nineteen characters were scored on 148 specimens (Table 2). The specimens scored included all the relatively complete specimens that seemed to belong in *Agropyron parishii* (including the holotype and isotype), plus several specimens that were puzzling, and others that I thought belonged in *Elymus glaucus*. For the numerical analyses, each specimen was considered to be a single Operational Taxonomic Unit (OTU) but, whenever feasible, inflorescence characters were measured on the same culm as vegetative characters and spikelet characters were measured on a spikelet from the mid-region of the same inflorescence.

Table 1. Nomenclatural history of *Agropyron parishii* and *A. parishii* var. *laeve.* Names within a column are based on the same type specimen. The unshaded cells with names refer to what is now regarded as a single species, *Elymus trachycaulus.* Shading indicates names that represent, or were thought by their users to represent, awned and unawned variants of *A. parishii.* Names in bold-face represent basionyms of later names in that column. *Agropyron pauciflorum* and *Elymus pauciflorus* are both illegitimate as names for *E. trachycaulus* because each had been used for another taxon prior to being applied to elements of *E. trachycaulus.*

Author	Year							
Schweinitz	1824		***Triticum pauciflorum***					
Link	1833			***Triticum trachycaulon***	***Triticum subsecundum***			
Vasey	1885	***Agropyron tenerum***						
Scribner & J.G. Smith	1897					***Agropyron parishii* var. *laeve***	***Agropyron parishii* var. *parishii***	
Hitchcock	1912	*Agropyron tenerum*				*Agropyron laeve*	*Agropyron parishii*	
Malte	1932			*Agropyron trachycaulum*				
Hitchcock	1934				*Agropyron subsecundum*			
Hitchcock	1935		*Agropyron pauciflorum*			*Agropyron parishii* var. *laeve*	*Agropyron parishii* var. *parishii*	
Gould	1947		*Elymus pauciflorus*		*Elymus pauciflorus* subsp. *subsecundus*	*Elymus pauciflorus* subsp. *laevis*	*Elymus stebbinsii*	
Shinners	1954			*Elymus trachycaulus*				
Hoover	1966					*Elymus laevis*	*Elymus laevis*	
A. Löve & D. Löve	1984		*Elymus trachycaulus* subsp. *trachycaulus*	*Elymus trachycaulus* subsp. *trachycaulus*	*Elymus trachycaulus* subsp. *subsecundus*	[Not mentioned]		
Barkworth	1993		*Elymus trachycaulus* subsp. *trachycaulus*	*Elymus trachycaulus* subsp. *trachycaulus*	*Elymus trachycaulus* subsp. *subsecundus*	*Elymus trachycaulus* subsp. *subsecundus*	*Elymus stebbinsii*	
Barkworth	1998		*Elymus trachycaulus* subsp. *trachycaulus*	*Elymus trachycaulus* subsp. *trachycaulus*	*Elymus trachycaulus* subsp. *subsecundus*	*Elymus trachycaulus* subsp. *subsecundus*	*Elymus stebbinsii* subsp. *stebbinsii*	***Elymus stebbinsii* subsp. *septentrionalis***

Table 2. Characteristics of *Elymus glaucus, E. stebbinsii* subsp. *stebbinsii*, and *E. stebbinsii* subsp. *septentrionalis* based on specimens included in this study. Values shown for continuous characters are minimum, **mean**, maximum of typical specimens, with minimum and maximum for depauperate specimens of the two subspecies of *E. stebbinsii* shown in parentheses. The data for *Elymus glaucus* reflect a bias inherent in the loan request which was for specimens that had been identified as *E. stebbinsii.*

	Character Description	*Elymus glaucus*	*Elymus stebbinsii* subsp. *stebbinsii*	*Elymus stebbinsii* subsp. *septentrionalis*
1	Thickness of the lowest internode and sheaths	0.7-**1.71**-2.5	1.2-**1.99**-2.8 (1.0-1.9)	1.8-**2.60**-3.6 (1.4-2.9)
2	Lowest visible node	28 glabrous, 8 pubescent	8 glabrous, 9 pubescent (5 glabrous, 1 pubescent)	36 glabrous, 2 pubescent (all 7 glabrous)
3	Lower leaf sheaths	34 glabrous, 2 pubescent	16 glabrous, 1 pubescent (all glabrous)	37 glabrous, 1 pubescent (all 7 glabrous)
4	Lower leaf sheath margins	34 glabrous, 2 ciliate	12 glabrous, 5 ciliate (5 glabrous, 1 ciliate)	34 glabrous, 4 ciliate (all 7 glabrous)
5	Auricle length (mm)	0.3-**1.26**-2.8	0.2-**1.43**-2.8 (0.2-2.8)	0.5-**1.31**-2.1 (0.4-2.0)
6	Ligule length (basal leaf) (mm)	0.3-**0.87**-1.8	0.5-**1.99**-5.0 (0.2-2.1)	0.2-**0.68**-1.3 (0.5-0.8)
7	Blade width (widest available) (mm)	2.2-**4.05**-6.0	2.6-**4.64**-8.0 (2.3-3.7)	2.2-**4.33**-6.5 (3.0-5.5)
8	Blade adaxial pubescence	9 glabrous, 11 scabrous, 7 slightly to moderately pilose, 8 densely pilose	3 glabrous, 1 scabrous, 3 slightly to moderately pilose, 10 densely pilose	6 glabrous, 12 scabrous, 15 slightly to moderately pilose, 12 densely pilose
9	Rachis internode length (average of 3 middle internodes) (mm)	7.3-**11.00**-16.5	16.3-**21.15**-27.0 (9.7-15.0)	9.5-**14.77**-20.3 (10.3-15.7)
10	Maximum number of spikelets per node	1-**1.25**-2	1	1
11	Spikelet length (longest available) (mm)	11.2-**15.13**-20.0	17.5-**22.25**-29.0 (12.1-16.0)	13.0-**16.74**-22.0 (11-19)
12	Maximum number of florets per spikelet	3-**4.5**-6	5-**7.0**-9 (3-5)	4-**4.80**-6 (3-6)
13	First glume length (mm)	6.0-**11.12**-20.0	6.0-**10.82**-15 (4.1-8.5)	7.3-**10.08**-12.8 (6.0-11.0)
14	Glume apex shape	35 acuminate to strongly tapering	13 acute, 4 acuminate	40 acute, 5 acuminate
15	Second glume length (mm)	6.0-**11.78**-16.0	7.0-**11.70**-15.0 (6.0-9.5)	7.9-**11.13**-13.8 (8.0-12.0)
16	First lemma length (mm)	8.0-**10.79**-13.0	9.5-**12.23**-14.5 (9.4-12.0)	9.0-**11.68**-15.0 (9.5-11.3)
17	First lemma awn length (mm)	2.0-**12.52**-26.0	1.5-**5.75**-11.6 (3.0-7.0)	8.0-**16.15**-25.0 (6.5-21.0)
18	First palea length (mm)	8.7-**9.85**-12.0	9.4-**11.50**-13.5 (8.2-11.5)	98.50-**10.81**-13.0 (8.8-10.3)
19	Anther length (mm)	2.0-**3.45**-4.6	4.6-**5.64**-7.0 (3.2-5.4)	4.2-**5.6**-7.1 (4.1-6.0)

There were several sets of duplicate specimens among those scored. These were deliberately kept in the analyses so as to provide a biological basis for evaluating the results of the numerical analyses.

The 19 characters scored included those mentioned by previous taxonomists as distinguishing the two taxa, plus some that my initial studies suggested might be of taxonomic value. Characters not available on a specimen were scored as missing. Only the continuous characters and floret number were used in the numerical analyses. The other characters were used to evaluate the groups suggested by these analyses and to assist in identifying specimens not included in the numerical analyses. Of the 148 specimens scored, 126 had data for all characters except floret number; 122 could be scored for all characters.

Four numerical procedures were used to explore the variation present: sequential agglomerative hierarchical nested cluster analysis (SAHN), principal component analysis (PCOMP), minimum spanning tree (MST), and discriminant analysis (DA). Principal component analysis was conducted on the correlation matrix. For MST and SAHN, the data were standardized by subtracting the mean and dividing by the standard deviation. Taxonomic distance (Sneath & Sokal 1973) was used as the distance measure.

Cluster analysis forces the OTUs into clusters. The taxonomic merit of these clusters can then be evaluated by examining whether they are supported by variation in characters not included in the analysis. Whenever feasible, different kinds of characters (*e.g.*, cytological, molecular) should be used in evaluating the predictive power of the clusters. Time and financial constraints limited me to characters evident on herbarium specimens.

Three clustering algorithms were employed: single linkage, complete linkage, and unweighted pair group mathematical average (UPGMA) (Sneath & Sokal 1973). Only UPGMA consistently placed members of duplicate OTU sets within the same major cluster; consequently only UPGMA results are presented.

Principal component analysis does not require the *a priori* assignment of OTUs to groups, but seeks to minimize the number of axes needed to portray the variation within a data set. It accomplishes this by constructing axes for a hyperdimensional space from linear combinations of the original data. The distribution of the OTUs along the first principal component (axis) accounts for as much of the variation in the original data set as possible, their distribution along the second principal component accounts for as much of the remaining variation as possible, with subsequent components doing the same for the ever-decreasing amount of variation left. The number of principal components needed to account for all the variation depends on the amount of correlation in the original data, fewer components being required if the data are highly correlated.

Although principal component analysis does not identify groups among the data, OTUs with different character correlations will be concentrated in different portions of the principal component space. A set of OTUs with similar character correlations will form a "cloud" in the character space. The taxonomic merit of such a set can then be evaluated by determining whether it is supported by the pattern of variation in characters not used in the analysis (Davis & Heywood 1963). Because only the projection of the OTUs onto the first three principal components was examined, MST was used to determine the closest neighbor of each OTU and these connections were superimposed on the PCOMP projection.

Discriminant analysis seeks to maximize the separation among pre-defined groups of OTUs based on linear combinations of the original data. These linear combinations, or functions, are then applied to each OTU and its group membership assessed. If the functions place the OTU closer to the centroid of a group other than its own group, that OTU is flagged as misclassified and the group with the closest centroid identified.

Because I had no independent criteria for assigning the OTUs to groups, I used the major clusters obtained from UPGMA cluster analysis as the initial groups. The membership of these groups was then modified to reflect the classification suggested by the first DA. This procedure was repeated until the discriminant functions placed all the OTUs in the group to which they had been assigned.

I then reevaluated the resulting groups of OTUs in terms of characters not used in the analyses. This resulted in the reclassification of a few OTUs. The data from these groups were then used to evaluate the specimens not included in the numerical analyses and a preliminary taxonomic treatment developed. After further review of the specimens, I examined the geographic and ecological distribution of the taxa that seemed to merit recognition, and summarized the morphological data for the three that were well represented in the study.

EXCEL (Microsoft 1997) was used to record the data and calculate univariate statistics. NTSYS (Rohlf 1993) was used for PCOMP, SAHN, and MST, and SYSTAT (SPSS 1997) for the discriminant analyses. To plot distributions, the latitude and longitude for each collection site represented was estimated using StreetAtlas (DeLorme 1997), Geographic Names Information System (U.S. Geological Survey 1993), or Wefald's (1995) program for converting township, range, and section data to latitude and longitude. Distribution maps were produced using Atlas Graphics version 2.1 (Strategic Mapping 1993).

RESULTS

CLUSTER ANALYSIS. Cluster analysis, using UPGMA, resulted in the formation of four major clusters (Figure 1) among the OTUs. The cluster containing the holotype of *Elymus stebbinsii* is labeled Sb, that containing what is designated below as the holotype of *E. stebbinsii* subsp. *septentrionalis* is labeled Sp. The other two clusters, A and B, consisted primarily of OTUs that belonged to the single spikelet variant of *E. glaucus*.

Groups A, B, and Sp were somewhat unstable. Measuring a different spikelet on a specimen sometimes moved a specimen from one cluster to another and the addition of a few specimens with missing anthers also altered the order in which the clusters linked together. Most of the movement involved groups A and B.

Surveying the specimens in each cluster, including looking at the characters not used in the analyses, convinced me that the clusters were taxonomically interesting entities, but that they were not identical with good taxa.

PRINCIPAL COMPONENT ANALYSIS. The first three principal components accounted for 37.1%, 17.1%, and 11.1%, respectively, of the total variance. Spikelet and floret characters contributed most to the first and second axes; basal culm diameter was the largest contributor to the third axis (Table 3).

Table 3. Coefficients of the five most significant characters in determining the location of OTUs on the first three principal components.

	Component 1	Component 2	Component 3
Largest contributor	Lemma length (0.8065)	Awn length (-0.6432)	Culm basal diameter (-0.6646)
Second contributor	Spikelet length (0.8952)	Second glume length (0.6070)	Anther length (0.6117)
Third contributor	Floret number (0.7740)	First glume length (0.6040)	First glume length (0.4240)
Fourth contributor	Rachis internode (0.7177)	Ligule length (0.5300)	Second glume (0.3633)
Fifth contributor	Second glume (0.6259)	Blade width (0.4577)	Awn length (0.3333)

The projection of the OTUs onto the first three components (Figure 2) revealed no strongly defined groups among the OTUs. The Sb group [using labels from the cluster analysis] was the most distinct, but its intra-group distances were also relatively large. The other three groups occupied basically different, but contiguous, portions of the principal component space, with the Sp group between groups A and B. Minimum spanning tree links provide an indication of the overlap among the groups. Ideally, the maximum number of intergroup links would be two per group, with two of the groups having only a single intergroup link, *i.e.*, 6 links for 4 groups. There were 21 intergroup links among the OTUs in this study. Group Sb had 5 (3 to Sp, 2 to A); group Sp had 11 (6 to B, 3 to Sb, and 2 to A); group A had 12 (8 to B, 2 to Sp, and 2 to Sb), and group B had 14 (8 to A, 6 to Sp).

DISCRIMINANT ANALYSIS. It was hard to determine, from looking at the specimens, which characteristics contributed most to the distinction between groups A and B, but comparison of the means for each cluster suggested that awn length was a major factor. For this reason, and because of the instability of the clusters, I decided to conduct two series of discriminant analyses, one in which A and B were considered as separate groups and one in which they were combined into a single group.

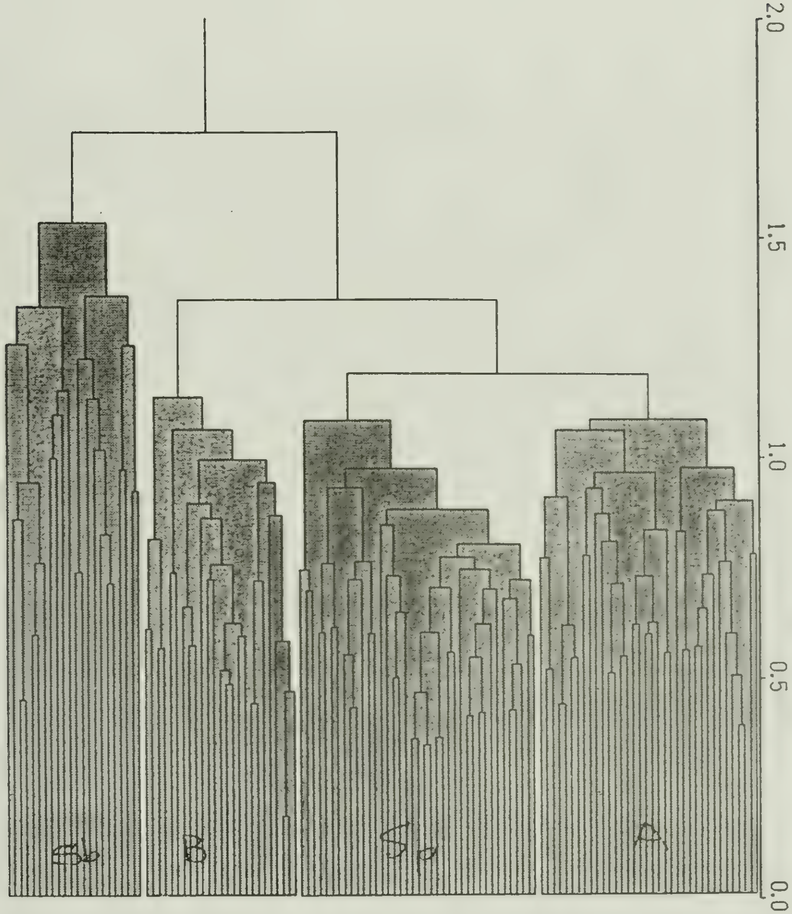


Figure 1. Results of UPGMA cluster analysis. The four major clusters are, from left to right, Sb, B, Sp, and A.

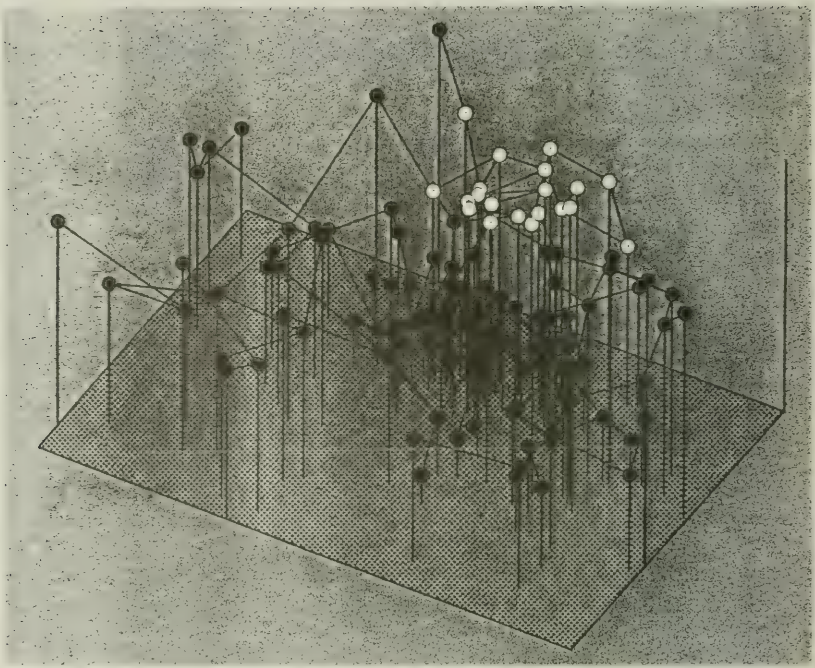


Figure 2. Projection of the OTUs onto the first three principal components. White - cluster A, light gray - cluster Sb, dark gray - cluster B, black - cluster Sp. Lines show links formed by Minimum Spanning Tree. The longest axis is the first axis, the vertical axis is the third axis.

Both series of DA disagreed with the cluster analysis in the placement of a few OTUs, but neither series considered any of the Sb group OTUs misclassified. In the 4-group analysis, 2 OTUs had to be reassigned before discriminant functions were generated that considered all OTUs correctly assigned, one from group Sp to group A, the other from cluster A to cluster B. Even then, jackknife analysis suggested that eight OTUs (9% of those in the analysis) were misclassified. With three groups, seven specimens had to be reassigned before the classification matrix showed no misclassifications, six from group A+B to group Sp, and one from group Sp to group A+B, the same OTU as was moved from group Sp to group A in the four-group analysis. Jackknife analysis resulted in a 5% misclassification rate.

Both series of discriminant analyses placed group Sp closer to the groups A and B (4-group series) or group A+B (3 group series) than to group Sb. Thinking that might be a reflection of awn length, I ran a 3-group analysis excluding the awn length character. This moved group Sp closer to group Sb, but it remained closest to the A+B group.

GROUP EVALUATION. To further evaluate the groups suggested by the numerical analyses, I obtained summary statistics for the four major groups, after modifying them to reflect the results of the discriminant analyses. The OTU that both series of discriminant analyses suggested should be reassigned was placed in the suggested group. The other supposedly misclassified OTUs were left in the group suggested by the cluster analyses.

Group Sb had more florets per spikelet, and longer ligules, rachis internodes, and spikelets, but shorter awns, than the other three groups. It resembled group Sp, and differed from groups A and B, in having longer anthers and somewhat longer florets. Group Sp differed from all other groups in having, on average, longer awns and thicker culms, but it overlapped the other groups in its extreme values. It differed from group Sb and resembled groups A and B in having relatively few florets per spikelet.

Group A differed from group B primarily in the longer length of its awns, glumes, and lemmas. The greatest difference between the two was in awn length, group A having longer awns. Group B also contained a number of OTUs with glumes that were unusually short relative to the first lemma.

QUALITATIVE CHARACTERS. Qualitative characters and the maximum number of spikelets per node were not included in the numerical analyses. Most were of little or no taxonomic value. Pubescent culm nodes were found on 50% of the OTUs in group Sb, but occurred, albeit less frequently, in the other three groups. Pubescent sheaths and ciliate sheath margins were uncommon in all groups. Adaxial blade vestiture varied from glabrous and smooth, through scabridulous to scabrous, to scabrous with some short pilose hairs, to densely pilose, but I could find no relationship between the vestiture and other characters.

Two characters, maximum number of spikelets per node and glume apex shape, were more interesting. Two spikelets per node were more common in groups A and B than groups Sb and Sp, although they were not common in any group. This last was partly an artifact of the loan request which specified taxa specimens identified as belonging to taxa that customarily have solitary spikelets. Glume apex shape was the most promising taxonomic character. All OTUs in group A had tapering or acuminate glume apices, as did 40% of those in group B and 21% of those in group Sb, but none of those in group Sp. In looking more closely at the variation in this character, I noted that the glumes of OTUs in groups Sp and Sb were often completely smooth or scabridulous only on the distal portion of the midvein. Glumes of groups A and B specimens were often scabridulous over more of the midvein as well as over other veins. In addition, the base of the glumes in groups Sp and Sb were more apt to have evident ridges over the veins whereas specimens in groups A and B usually had smooth glume bases. There were, however, exceptions in both directions.

Another character that tended to distinguish groups Sb and Sp from groups A and B, the shape of the palea apex, became apparent during the course of this study. In OTUs of groups Sb and Sp, the palea veins scarcely converged and the end of the intercostal tissue was truncate. In most OTUs of groups A and B the veins converged more strongly and the intercostal tissue had a V-shaped notch, making the palea apices look acute and bifid. Examination of specimens of *Elymus glaucus* and *E. trachycaulus* in UTC from Utah and Idaho suggested that converging paleal keels and a slightly notched palea apex are common in these two species. According to this criterion, most specimens referable to groups A and B belonged to *E. glaucus* or *E. trachycaulus*, but some belonged to group Sb or Sp. Unfortunately, there is some variation in the palea character within a plant. Moreover, Connor (1994) found that, in New Zealand species of *Elymus*, the blunt and truncate to slightly retuse palea apex appears to be a dominant single gene character, suggesting that this palea character should be used with caution.

I used the results of the various analyses to develop tentative descriptions and diagnoses for four taxa, corresponding to the four groups, and then reviewed all the specimens available to me to determine in which group I would place them. In doing so, I was aware that the characters analyzed had been selected for their ability to distinguish specimens of *Elymus stebbinsii* from other taxa with which it had been confused. There was no *a priori* reason why groups A and B should be taxonomically significant or homogeneous.

The review showed that all the specimens in group Sb were referable to Scribner & Smith's *Agropyron parishii* var. *parishii*, but it did not include some of the less robust specimens that I would have included in that taxon. The specimens occur primarily in the Coast Ranges, the Tehachapi Mountains, and the Transverse Ranges.

Group Sp consisted of plants that differed from group Sb plants primarily in having longer awns and fewer florets (on average). They also had a somewhat different geographic distribution, occurring primarily on the west slopes of the Sierra Nevada and in the southern Cascade Mountains (Hunt 1974), often in yellow pine forests. As with group Sb, some less robust specimens that I would have assigned to group Sp were placed in groups A and B by the numerical analyses. I concluded that the specimens in group Sp should be regarded as part of *Elymus stebbinsii* but that they should be recognized as representing a distinct subspecies because of their morphological and distributional differences from specimens in the group that included the holotype of *E. stebbinsii*.

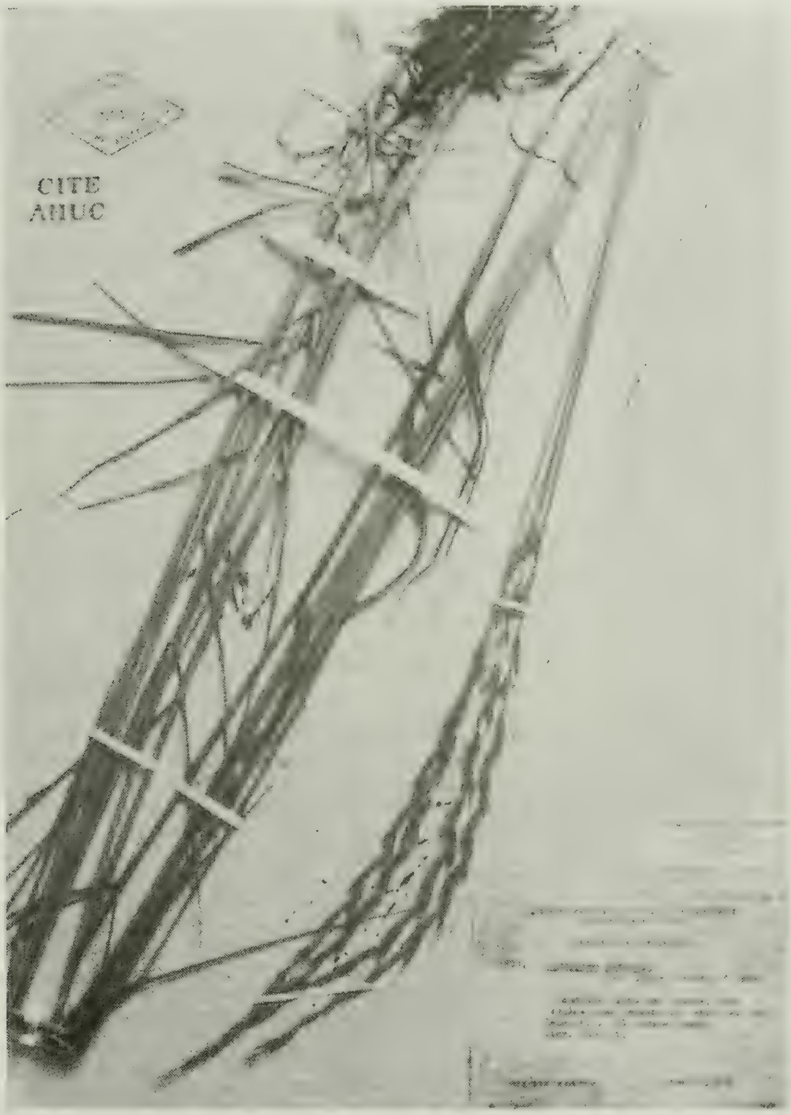
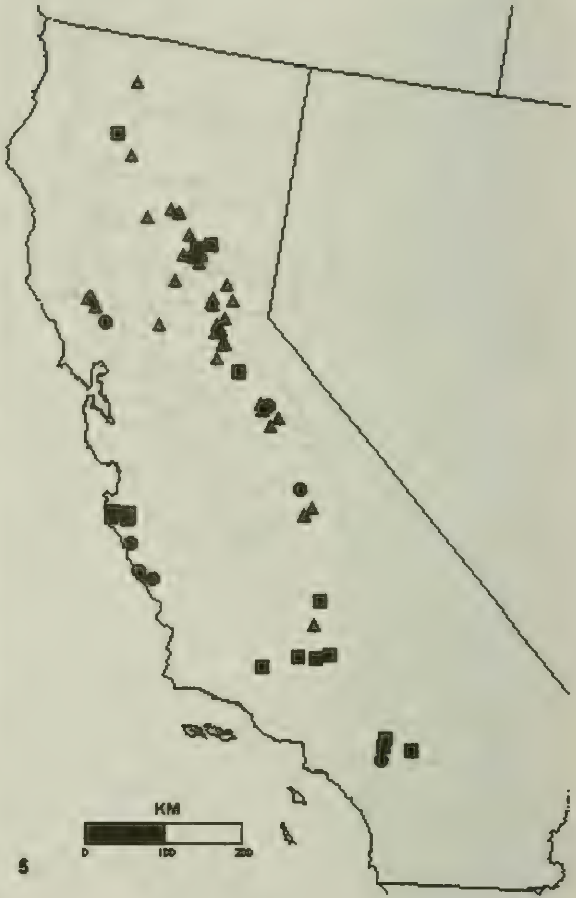


Figure 3. Holotype of *Elymus stebbinsii* subsp. *septentrionalis*. Note the robust culm and widely spaced spikelets.

4



5

Figure 4. Spikelet from holotype, showing glumes and palea apex.

Figure 5. Distribution map of *Elymus stebbinsii*. Squares - specimens for which the subspecies could not be determined, circles - subsp. *stebbinsii*, triangles - subsp. *septentrionalis*.

Most group A and B OTUs belonged to *Elymus glaucus*, but both groups included some depauperate specimens of the two *E. stebbinsii* subspecies. These depauperate specimens had the long anthers and acute, relatively smooth glumes characteristic of *E. stebbinsii*, but had thinner culms, shorter spikelets and spikelet parts, and proportionately shorter glumes, than typical members of the species. Most were relatively long-awned, but a few had short awns. Their geographic distribution mimicked that of the two subspecies of *E. stebbinsii*.

I re-analyzed the data after removing the specimens that I was confident did not correspond to either variety of *Agropyron parishii*. The results were not encouraging. Cluster analysis identified three major clusters. Two of these corresponded in general to groups Sb and Sp, but the third cluster contained some of the OTUs that had previously been placed in group Sb or Sp. Because there was no hint that further analyses of the same specimens would clarify the taxonomy of the specimens involved, I halted the study at this stage.

CONCLUSIONS

Completing a taxonomic study of morphologically similar taxa solely on the basis of herbarium specimens is frustrating. One cannot assess populational variation, nor the extent to which a taxon's morphology may be modified by various kinds of stress. My original goal was simply to determine whether there was a taxon corresponding to Scribner & Smith's description of *Agropyron parishii* var. *laeve* but, to address it, it became necessary to re-evaluate the morphological limits of *Elymus glaucus* and *E. trachycaulus*.

The results obtained in this study support recognition of two taxa within *Elymus stebbinsii*. One, corresponding to group Sb, consists of shortly awned plants with large spikelets having 6-9 florets per spikelet and occurs in the Coast and Transverse Ranges. The other, corresponding to group Sp, is a longer-awned taxon with somewhat fewer florets per spikelet that occurs to the north and east of the Great Central Valley. It is possible that the long-awned taxon corresponds to Scribner & Smith's var. *laeve* taxon and that the choice of a type was simply unfortunate, but this cannot be determined with certainty. They (Scribner & Smith 1897) did not include anther length, the most consistent reliable character for distinguishing between *E. trachycaulus* and *E. stebbinsii*, in their description of *Agropyron parishii*, nor did they provide distributional information for the taxon. Nevertheless, Gould having recognized that the holotype of *A. parishii* var. *laeve* belongs in *E. trachycaulus*, a new epithet must be found for the long-awned taxon in *E. stebbinsii*.

Although the numerical analyses place the long-awned taxon closer to *Elymus glaucus* and *E. trachycaulus* than *Agropyron parishii* var. *parishii*, the shape of its glumes and palea suggest that it is genetically closer to var. *parishii* than either of the other two taxa. This is confirmed by its similarity to var. *parishii* in the distinctive characters of typical members of that taxon, *i.e.*, the robust, somewhat decumbent culms, the widely spaced spikelets, and long anthers. Because the long-awned taxon tends to be geographically distinct from var. *parishii* (Figure 3), I propose that it be recognized as *E. stebbinsii* subsp. *septentrionalis*, thereby automatically creating the name *E. stebbinsii* subsp. *stebbinsii* for *A. parishii* var. *parishii.* No specimens of either subspecies of *E. stebbinsii* were found from San Diego County, location of the type of *A. parishii* var. *laeve.*

Elymus stebbinsii Gould subsp. ***septentrionalis*** Barkworth, *subsp. nov.* HOLOTYPUS: U.S.A. California: El Dorado County, 0.5 miles west of Omo Ranch Post Office, 22 June 1956, *Beecher Crampton 3598* (AHUC 22602 [Figures 3,4]).

Differt a subsp. *stebbinsii* arista lemmatis longiore et nodo infirmo persaepe glabro.

Gramen perennis. Culmi laxe fasciculati, erecti vel basi decumbentibus, 70-130 cm altus, internodio infirmo (1.4)1.7-3.6 mm crasso; nodi persaepe glabro. Foliorum vaginae persaepe glabrae, margines fauci ciliati; auriculae 0.4-2.6 mm longae, falcatae; ligulae 0.25-1.25 mm, truncatae, ciliatae; laminae 2.2-6.5 mm latae, glabrae, scabrae, vel pilosae. Inflorescentia spica una spicula in quoque nodo; internodia 9.5-20.3 mm; spiculae (11)13-22 mm longa, flosculi 4-6; gluma inferior (6.0)7.7-12.8 mm, acuta, gluma superior parum longior; lemma infima 9.5-15.0 mm, terminans arista (6.5)11-25 mm, lemmae longior vel paulo brevioribus; palea lemmae paulo brevioribus; antherae 4.1-7.1 mm longae.

Paratypes: U.S.A. California: Butte County, along Big Bar Road, about 1 mile south-west of Coyote Gap, 8 July 1987, *Lowell Ahart 5805* (CHSC 42952); El Dorado County, 1.8 miles west of Omo Ranch Post Office, 22 June 1956, *Beecher Crampton 3590* (UC 1040715); Lake County, 1 mile east of Loch Lomond, 26 June 1956, *Beecher Crampton 3626* (AHUC 22604); Placer County, Shirttail Canyon, 6.5 miles west of Iowa Hill, 15 June 1955, *Beecher Crampton 2895* (AHUC 21154).

Differing from subsp. *stebbinsii* in its longer lemma awns and almost always glabrous lowermost culm node.

Perennial grass. Culms loosely clustered, erect or decumbent at the base, 70-130 cm tall; lower internodes (1.4)1.7-3.6 mm thick, the lowermost node almost always glabrous. Leaf sheaths almost always glabrous, the margins of the throat ciliate; auricles 0.4-2.6 mm long, falcate; ligules 0.25-1.25 mm, truncate, ciliate; blades 2.2-6.5 mm wide, glabrous, scabrous, or pilose. Inflorescence a spike with one spikelet per node; middle internodes 9.5-20.3 mm; spikelets (11)13-22 mm long, with 4-6 florets. Lower glume (6.0)7.7-12.8 mm long, acute; upper glume slightly longer; lowest lemma 9.5-15.0 mm, terminating in an awn (6.5)11-25 mm long, longer or slightly shorter than the lemma; palea slightly shorter than the lemma; anthers 4.1-7.1 mm long.

Typical members of the two varieties of *Elymus stebbinsii* are robust plants with thick, decumbent culms. Among the specimens studied, however, there were several slender, delicate plants that had the distant spikelets, truncate palea apices, and acute glumes characteristic of *E. stebbinsii*, but the glumes that tended to be shorter in proportion to the first lemma than those of typical specimens (most fell into group B). I considered recognizing them as a distinct taxon but decided against doing so because there were both awned and unawned specimens present and the distribution of these mimicked that of the robust specimens. In addition, even when the non-*stebbinsii* OTUs were removed from the data set, the delicate specimens did not form a distinct cluster, but occurred within the Sb and Sp clusters. I strongly recommend further study of such plants. They may be nothing more than depauperate plants, but the lack of continuity between them and typical representatives of the two subspecies is disconcerting.

Representatives of the short-glumed variant include Kern County, swale at head of Mill Creek, 27 July 1965, *Ernest C. Twisselmann 11239* (AHUC 32447); Mariposa County, above Wawona Road Tunnel, 17 July 1936, *Lyman Benson 7893* (POM 295836); Placer County, along southeast bank of American River, 1.5 miles northeast of bridge on Colfax-Iowa Road, 22 June 1952, *G.L. Stebbins, Jr. 5102* (CAS 376178); Plumas County, near Lewisia rock in Feather River Canyon, 12 June 1968, *John Thomas Howell 44561 and Gordon H. True* (CAS 633387); Siskiyou County, canyon north of Willow Creek, 5 miles west of Gazelle, 31 May 1942, *A.A. Beetle 3406 and G.L. Stebbins, Jr.* (AHUC 7519); Yuba County, about 2 miles east of Challenge, 25 June 1979, *Lowell Ahart 1946*.

The two subspecies of *Elymus stebbinsii* are generally geographically separated but *Ahart 5887* (CAS 916837, CHSC 43290), from Butte County, was exceptional in having the characteristics of subsp. *stebbinsii* despite coming from northeastern California. Illustrations of both subspecies of will be included in the *Manual of Grasses for the Continental United States and Canada* (Barkworth *et al.*, in prep.).

Glume shape is the best character for distinguishing *Elymus stebbinsii* from specimens of *E. glaucus* with solitary spikelets and long anthers. Palea shape and basal culm thickness also appear to be helpful (Table 2). A few specimens suggest that the two species may form partially fertile hybrids (*e.g.*, San Antonio Mountains, Browns Flat, dry open ground under pine, 1 July 1917, *I.M. Johnston 1518* [DS 83847]; Tuolumne County; Strawberry, 5300 ft, June 1951, *A. Haig s.n.* [AHUC 14340]; Kern County, East fork of Upper San Emigdio Canyon, Douglas oak-pinyon association, 22 June 1961, *Ernest C. Twisselmann 6284* [CAS 523141]).

Distinguishing *Elymus trachycaulus* from *E. stebbinsii* does not present a problem if anthers are present. Distinguishing it from *E. glaucus* is often harder, even if anthers are present. I wish I could state that I now know how to separate herbarium specimens of the two taxa with confidence. I cannot. Some specimens are easy to place in one species or the other, but there are a disturbingly large number with solitary spikelets that I find extremely hard to identify with any degree of confidence.

There were two specimens examined during this study that were particularly interesting. I include information about them here in the hope that it will stimulate others to examine them, and the sites from which they were obtained, in greater detail. One such specimen was El Dorado County, 2.6 mi southeast of Placerville, roadcut, shaded slope forested by yellow pine and oak, June 22, 1956, *Beecher Crampton 3617* (AHUC 22601). This was a robust specimen (culm 155 cm tall, basal diameter 3.1 mm) with well-spaced, long-awned spikelets (internodes 14 mm, spikelets 15 mm, awns to 18 mm), truncate paleas, and long (5.7 mm) anthers. The distinctive features were its long spikes (around 25 cm) and short (about 8 mm), stiff, almost truncate glumes reminiscent of *Thinopyrum intermedium*. Of the Triticeae with which

I am acquainted, it is closest to *E. stebbinsii* subsp. *septentrionalis*, but it is an unusual representative of that taxon. Another interesting specimen was Monterey County, Pico Blanco, May-June 1901, *J. Burtt Davy 7364* (UC 607791). It belongs in *E. stebbinsii* subsp. *stebbinsii*, but it has narrow, convolute leaves that distinguished it from all other specimens of the taxon.

Table 2 summarizes data obtained for *Elymus stebbinsii* and *E. glaucus* obtained in this study. The data for *E. glaucus* came from a very biased sample. All the specimens involved came from California although the species extends north to Alaska and east to the Central Plains. In addition, they were included in the study because they had been identified as *E. stebbinsii.* This criterion biased the sample towards plants with large, solitary spikelets and longer anthers than is typical for the species. No data are presented for *E. trachycaulus* because very few were included in the numerical portion of the study. The key to Californian species of *Elymus* that follows reflects the results of this study and the decision to include quackgrass in *Elymus* as *E. repens.*

KEY TO THE CALIFORNIAN SPECIES OF *ELYMUS*

1. Glumes absent; spikelets usually 3-4 per node........................*E. californicus*
1' Glumes present, lanceolate to setaceous; spikelets usually 1-3(4) per node.
 2. Rachis disarticulating at maturity; glumes narrow to setaceous, terminating in an awn 25-100 mm long.
  3. Glumes 3-many cleft; auricles conspicuous, usually around 1 mm long..*E. multisetus*
  3' Glumes entire or 2-cleft, rarely 3-cleft with 2 short lateral awns; auricles less than 1 mm or wanting........................*E. elymoides*
   4. Spikelets 3 at each node, only the central spikelet with fertile florets.......................*E. elymoides* subsp. *hordeoides*
   4' Spikelets 2 at each node or, if more, the lateral spikelets with one or more fertile florets.
    5. All florets in the spikelet similar... *E. elymoides* subsp. *longifolius*
    5' First floret of some lower spikelets glume-like, the spikelets consequently appearing to have 3 glumes.
     6. At least one glume at the lower nodes 2-cleft. ....*E. elymoides* subsp. *elymoides*
     6' All glumes entire............... *E. elymoides* subsp. *californicus*
 2' Rachis not disarticulating at maturity except in *E. scribneri*; glumes lanceolate, sometimes narrowly so, unawned or the awn less than 10 mm long.
  7. Spikelets 2 or more at most nodes.
   8. Inflorescence nodding; glumes curving at the base, exposing the base of the first floret; lemma awns arcuately diverging. ....*E. canadensis*
   8' Inflorescence erect; glumes straight at the base, concealing the base of the first floret. ....*E. glaucus*
    9. Lemma awns less than 9 mm long..... *E. glaucus* subsp. *virescens*
    9' Lemma awns 10-30 mm long.

10. Lower leaf sheaths smooth or scabrous, not pubescent.......................... *E. glaucus* subsp. *glaucus*
10' Lower leaf sheaths pubescent. ......*E. glaucus* subsp. *jepsonii*
7' Spikelets solitary at all or most nodes.
11. Plants strongly rhizomatous; anthers 3-6 mm long.
12. Glumes rounded at the base, strongly keeled above, the midveins smooth below and scabrous above..............*E. repens*
12' Glumes more or less rounded throughout their length, the midvein evenly scabrous from the base or less so above...*E. lanceolatus*
11' Plants cespitose, not rhizomatous; anthers 1-5 mm long.
13. Lemmas with arcuately diverging awns.
14. Inflorescence drooping; plants not subalpine or alpine (doubtfully present in California)...........*E. arizonicus*
14' Inflorescence straight; plants of subalpine and alpine habitats.
15. Rachis internodes 8-10 mm; rachis not disarticulating at maturity............................*E. sierrae*
15' Rachis internodes 3.5-8.0 mm; rachis disarticulating at maturity......................... *E. scribneri*
13' Lemmas unawned or the awn straight.
16. Glumes acute, unawned; rachis internodes 16-21 mm; anthers 4.2-7.2 mm...................... *E. stebbinsii*
17. Lemma awns 1.5-11.5 mm; florets 5-9 per spikelet; leaf sheaths often pubescent......................*E. stebbinsii* subsp. *stebbinsii*
17' Lemma awns (8)12-25 mm long; florets 4-6 per spikelet; leaf sheaths occasionally pubescent................*E. stebbinsii* subsp. *septentrionalis*
16' Glumes acute or tapering to acuminate or awned; rachis internodes 4.0-16.5 mm; anthers 0.8-4.6 mm (anthers short if glumes acute).
18. Glumes acuminate, often awned, the veins usually equally scabridulous throughout; anthers 2.0-4.6 mm (see above for varieties).....*E. glaucus*
18' Glumes acute to acuminate, the midvein often more scabridulous than the others; anthers 0.8-2.5 mm...........................*E. trachycaulus*
19. Lemma awns longer than the body, 8-30 mm..........*E. trachycaulus* subsp. *subsecundus*
19' Lemma awns shorter than the body, up to 7 mm. ....*E. trachycaulus* subsp. *trachycaulus*

ACKNOWLEDGMENTS

I thank the curators of AHUC, CAS, CHSC, DAV, DS, GH, JEPS, POM, RSA, SD, UC, and US for making the specimens in their care available to me, Michael Curto for drawing my attention to the problem in the first place and for subsequent discussions concerning this and other grasses. I am particularly grateful to Dr. Jack Maze for the numerous suggestions he made on my initial manuscript and for his comments on the resulting second version. I am also grateful to Dr. Adolf Ceska and Harvey Ballard who made additional suggestions for improvement, Dr. Kathleen Capels whose eagle eyes caught inconsistencies and editorial errors that had escaped my notice, and Dr. Mark Damen who provided a Latin description that classicists can read without cringing. I am, of course, responsible for any remaining errors or lack of clarity, but there would have been more had it not been for the generous assistance of these individuals.

LITERATURE CITED

Abrams, L. 1940. *Illustrated Flora of the Pacific States*. Stanford University Press, Stanford, California.

Barkworth, M.E. 1993. *Elymus*. Pp. 1253-1256 *in* J.C. Hickman (Ed.), *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley, California.

Barkworth, M.E. 1996. The *Elymus trachycaulus* complex in North America: many questions, few answers. Pp. 189-194 *in* Wang, R.R.-C., K.B. Jensen, & C. Jaussi (Eds.), Proc. Second International Triticeae Symposium, Forage and Range Laboratory, U.S.D.A.-A.R.S., Logan, Utah.

Connor, H.E. 1994. Indigenous New Zealand Triticeae: Gramineae. New Zealand J. Bot. 32:125-154.

Davis, P.H. & V.H. Heywood. 1963. *Principles of Angiosperm Taxonomy*. D. Van Nostrand Company, Inc., Princeton, New Jersey.

DeLorme. 1997. Street Atlas USA, version 5.0. DeLorme Mapping, Freeport, Maine.

Dremann, C. 1995. *Bromus carinatus* and *Elymus glaucus* storage, longevity, genetic changes, and ecotypical variations. Grasslands 5:2-5.

Gould , F.W. 1947. Nomenclatural changes in *Elymus* with a key to the Californian species. Madroño 9:120-128.

Hall, H.M. 1902. A botanical survey of San Jacinto Mountain. Univ. Calif. Publ. Bot. 1:1-140.

Hitchcock, A.S.. 1912. Gramineae. Pp. 82-189 *in* W.L. Jepson, *A Flora of California*, part 3. Associated Students Store, University of California, Berkeley, California.

Hitchcock, A.S. 1935. *Manual of Grasses of the United States*. U.S.D.A. Misc. Publ. 200, Washington, D.C.

Hitchcock, A.S. 1951. *Manual of Grasses of the United States*. Ed. 2, revised by A. Chase. U.S.D.A. Misc. Publ. No. 200, Washington, D.C.

Holmgren, P.K., N.H. Holmgren, & L.C. Barnett. 1990. *Index Herbariorum*. Part 1: The herbaria of the world. Ed. 8. International Association for Plant Taxonomy, New York Botanical Garden, Bronx, New York.

Hoover, R.F. 1966. Miscellaneous new names for California plants. Leafl. W. Bot. 10:337-350.

Hunt, C.B. 1974. *Natural Regions of the United States and Canada*. W.H. Freeman and Company, San Francisco, California.

Lamarck, J.B.A.P.M. 1791. *Tableau Encyclopédique et Méthodique des Trois Règnes de la nature*. Chez Pancoucke, Paris, France.

Microsoft Corporation. 1997. Excel 97. Microsoft Corporation, Bellevue, Washington.

Munz, P.A. 1959. *A California Flora*. University of California Press, Berkeley, California.

Rohlf, F.J. 1993. NTSYS-pc: numerical taxonomy and multivariate analysis system, version 1.80. Exeter Software, Setauket, New York.

Scribner, F.L. & J.G. Smith. 1897. Native and introduced species of the genera *Hordeum* and *Agropyron*. U.S.D.A. Div. Agrostol. Rep. Agrostol. 4:23-36.

Shinners, L.H. 1954. Notes on North Texas Grasses. Rhodora 56:25-44.

Sneath, P.A. & R.R. Sokal. 1973. *Numerical Taxonomy: The Principles and Practice of Numerical Taxonomy*. W.H. Freeman, San Francisco, California.

Snyder, L.A. 1950 Morphological variability and hybrid development in *Elymus glaucus*. Amer. J. Bot. 37:628-636.

SPSS. 1997. SYSTAT 7.0 for Windows. SPSS Inc., Chicago, Illinois.

Strategic Mapping. 1993. Atlas GIS, version 2.1. Strategic Mapping, Inc., Santa Clara, California.

U.S. Geological Survey, National Mapping Division. 1993. USGeoData: Geographic Names Information System, Earth Science Information Center, Reston, Virginia.

Wefald, M. 1995. TRS2LL.EXE, a computer program for converting between township, range, section data and latitude and longitude in the western United States. Available by Email from stipoid@cc.usu.edu.

Phytologia (November 1997) 83(5):366-370.

CHROMOSOME STUDIES AND TAXONOMIC CONSIDERATIONS IN *ACILEPIDOPSIS* (VERNONIEAE, ASTERACEAE)

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ABSTRACT

Chromosome number and karyotype are reported for the first time in *Acilepidopsis echitifolia* (Mart. *ex* DC.) H. Rob. The species presents a somatic chromosome number of $2n=8x=72$, with the karyotype composed of 46 metacentric, 16 submetacentric and 10 subtelocentric-acrocentric chromosomes. At meiosis, *A. echitifolia* always shows 36 bivalents, interpreted here as an allopolyploid based on $x=9$. The basic number found in *Acilepidopsis* supports its generic status and suggests a clear relationship with members of Vernonieae from the Eastern Hemisphere.

KEY WORDS: Asteraceae, Vernonieae, *Acilepidopsis*, pollen, chromosomes, relationships

Acilepidopsis H. Rob. has been recently removed from the American *Vernonia* on the basis of the pollen, glands, stem base, and style type (Robinson 1989, 1990). The genus contains a single species, *A. echitifolia* (Mart. *ex* DC.) H. Rob., which lives in moist soils from northern Argentina, Bolivia, Paraguay, and southern Brazil.

The pollen of *Acilepidopsis* is triporate, lophate, entirely covered of similar sized areoles, with smooth crests of the muri lacking a perforated tectum (Figure 1). Such pollen has been called type "E" by Jones (1981) and is present in many species of the Eastern Hemisphere. On the other hand, most American taxa have tricolporate pollen, with several different types named A, B, C, and D (Jones 1979a).

The pollen morphology of *Acilepidopsis echitifolia* has suggested that it would be more closely related to Old World members placed in *Vernonia* Schreb. than to other American taxa. Robinson (1989), in the original description of the genus, considered that cytological and chemical data could confirm the relationship of *A. echitifolia* to African members of Vernonieae. From the cytological viewpoint, the species of both hemispheres may be distinguished primarily on the basic chromosome number. Old World taxa present x=9 and x=10, while the American entities mainly have a base number x=17 (Jones 1979b), although have been also reported x=16, x=15, x=14, and x=10 (Dematteis 1997).

In the present study the somatic and meiotic chromosomes of *Acilepidopsis echitifolia* are analyzed for the first time. The results are discussed in relation to its taxonomic position and relationships.

Chromosome preparations were obtained following the methodology suggested by Dematteis (1997). Nomenclature used for the karyotype description is that proposed in Levan *et al.* (1964). The origin of the plants examined is: PARAGUAY. Dept. Amambay: 30 km N of route 5, on the road to Bella Vista, *M. Dematteis & A. Schinini 872*. Voucher specimens have been deposited in the herbarium of the Instituto de Botánica del Nordeste (CTES).

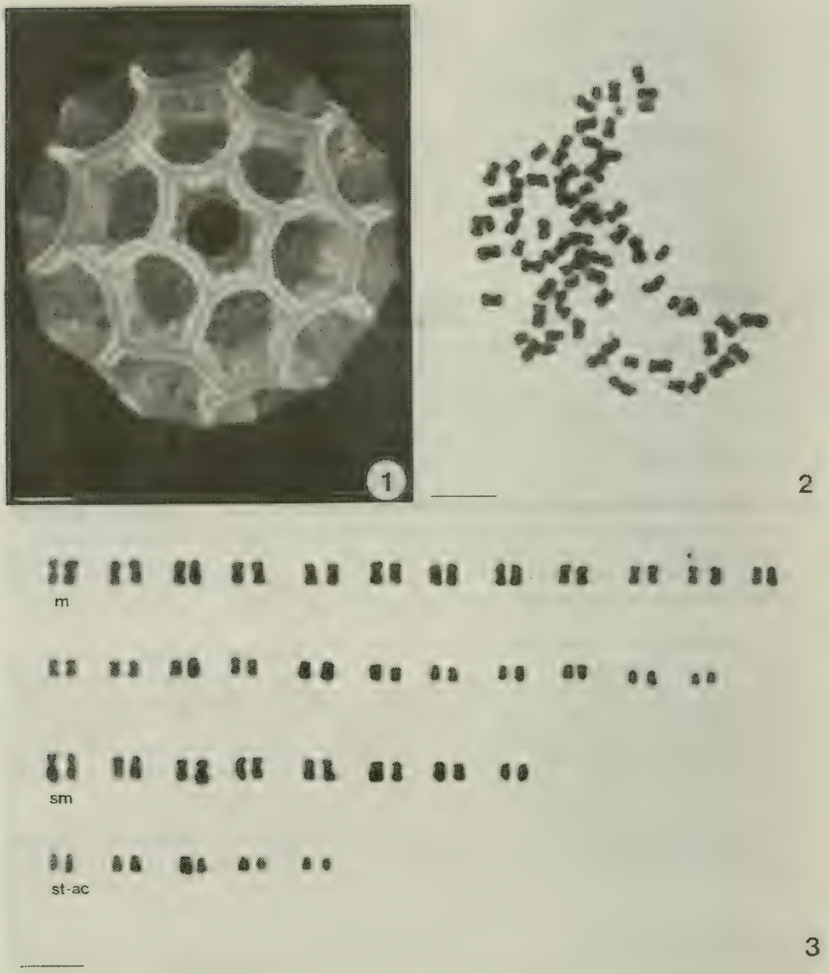
Acilepidopsis echitifolia was found to be octoploid with 2n=72 (Figure 2). The karyotype was composed of 46 metacentric (m), 16 submetacentric (sm), and 10 subtelocentric-acrocentric (st-ac) chromosomes (Figure 3). Chromosome size ranged from 1.17 to 2.55 µm, with a mean length of 1.81 µm. Total karyotype length was 130.58 µm. The satellite was observed in the short arm of the metacentric pair N° 11 (Figure 3). At meiosis, *A. echitifolia* showed a regular behaviour, forming invariably 36 bivalents. According to this observation, *A. echitifolia* would likely be an allopolyploid species.

The basic chromosome number x=9 found in *Acilepidopsis* supports its generic status and a probable close relationship with African taxa, in which this number is the more frequent. However, in contrast to the latter, *A. echitifolia* possesses a relatively high ploidy level (8x). In Old World species, polyploidy is uncommon, and only tetraploids and hexaploids have been reported (Jones 1979b).

Acilepidopsis echitifolia presents a comparatively large number of subtelocentric-acrocentric chromosomes. This feature clearly separates *Acilepidopsis* from other American genera of Vernonieae, such as *Lessingianthus* H. Rob., *Lepidaploa* (Cass.) Cass., and *Vernonanthura* H. Rob., which in majority have metacentric and submetacentric pairs (Dematteis & Fernández 1998). The subtelocentric chromosomes seem to be exceptional in these groups, and when present, the number of pairs is always lower than in *Acilepidopsis*.

In addition to the chromosomal information, chemical data available for the tribe also support the generic status of *Acilepidopsis*, since it is the only member of Vernonieae yet known to have lignans (Bohlmann *et al.* 1981).

The basic number x=9 has not been previously reported for any American entity. However, it may be expected in other New World groups having type "E" pollen, because there is an evident relationship between pollen morphology and chromosome number (Robinson 1992a). The genera with tricolporate pollen show basic chromosome numbers x=17, x=16, x=15, and x=14. The genera that possess triporate pollen types have base numbers x=8, x=9, x=10, x=11, and x=13. The two other genera that may have x=9 are *Mesanthophora* H. Rob. and *Pacourina* Aubl., which are the other American groups with type "E" pollen.



Figures 1-3. *Acilepidopsis echitifolia*. 1. Pollen grain, view showing pore. 2. Somatic chromosomes, $2n=72$. 3. Karyotype, 46m + 16sm + 10st-ac. Scale=5µm.

Acilepidopsis may be more closely related to *Mesanthophora*, a monotypic genus described for Paraguay (Robinson 1992b) and since discovered in Bolivia. Despite the identical pollen type, the genera differ considerably in many other morphological features. *Acilepidopsis* is a pubescent plant covered with reddish glands, has sessile heads, 8-13 flowered, placed in the axils of leafy branches; meanwhile, *Mesanthophora* is a glabrous plant with pedunculate, 90-100 flowered heads, located in a supra-axillary position.

A particular feature noticed in *Acilepidopsis* since its description is the unusual sclerified pointed base of the anther thecae, which is otherwise known in the more distantly related *Piptocarpha* (x=17).

Additional chromosome studies, especially in genera with triporate pollen, could provide a better understanding of the relationships between *Acilepidopsis* and other American and African genera of Vernonieae.

ACKNOWLEDGMENTS

The pollen specimens were prepared by Barbara Eastwood using facilities of the Smithsonian Botany Department Palynological Laboratory. The pollen photographs were taken by Brian Kahn of the National Museum of Natural History Laboratory using a Hitachi S-570 scanning electron microscope.

REFERENCES

Bohlmann, F., L. Müeller, R.K. Gupta, R.M. King, & H. Robinson. 1981. Hirsutinolides from *Vernonia* species. Phytochemistry 20(9):2233-2237.

Dematteis, M. 1997. Números cromosómicos y cariotipos de algunas especies de *Vernonia* (Asteraceae). Bol. Soc. Argent. Bot. 33(1-2):85-90.

_____ & A. Fernández. 1998. Karyotypes of seven South American species of *Vernonia* (Asteraceae). Cytologia 63: in press.

Jones, S.B. 1979a. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the New World. Rhodora 81:425-447.

_____. 1979b. Chromosome numbers of Vernonieae (Compositae). Bull. Torrey Bot. Club 106:79-84.

_____. 1981. Synoptic classification and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the Old World. Rhodora 83:59-75.

Levan, A., K. Fredga, & A.A. Sandberg. 1964. Nomenclature for centromeric position on chromosomes. Hereditas 52:201-220.

Robinson, H. 1989. *Acilepidopsis*, a new genus of Vernonieae from South America (Asteraceae). Phytologia 67(4):289-292.

_____. 1990. Studies in the *Lepidaploa* Complex (Vernonieae: Asteraceae) VII. The genus *Lepidaploa*. Proc. Biol. Soc. Wash. 103:464-498.

_____. 1992a. The Asteraceae of the Guianas, III: Vernonieae and restoration of the genus *Xiphochaeta*. Rhodora 94:348-361.

_____. 1992b. *Mesanthophora*, a new genus of Vernonieae (Asteraceae) from Paraguay. Novon 2:169-172.

Phytologia (November 1997) 83(5):371-383.

A NEW PLANT COMMUNITY TYPE IN SOUTHEAST TEXAS RELATED TO BAYGALLS

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ABSTRACT

An area of seep-fed muck bogs paralleling Prairie Branch in Walker County, Texas, has physical and vegetative features most similar to a "baygall," a distinctive and recurring wetland community in the southeastern United States. The Prairie Branch community is dominated by *Viburnum nudum* (possum haw viburnum), *Nyssa sylvatica*, *Myrica cerifera*, *Liquidambar styraciflua*, and *Smilax laurifolia*, but most of the other woody (as well as herbaceous) species characteristic of baygalls are absent. This community is described here as a "possum haw bog," situated at the western edge of the eastern deciduous forest, where it is speculated that decreased precipitation, in part, has correspondingly reduced the potential species diversity of the bog as well as other communities in the vicinity.

KEY WORDS: baygall, possum haw bog, *Viburnum nudum*, community ecology, Texas

Baygalls are a characteristic wetland community of the Atlantic and Gulf Coastal Plains extending into southeastern Texas (Harper 1914; Wells & Shunk 1928; Watson 1979; Christensen 1988; Bridges & Orzell 1989; Harcombe *et al.* 1993; Brooks *et al.* 1993; Weakley *et al.* 1998). They are variable over their range but are generally characterized by such woody species as *Magnolia virginica* (sweet bay) and *Ilex coriacea* (gallberry holly), for which the community is named, *Nyssa sylvatica*, *Rhododendron* spp., *Ilex opaca*, *Acer rubrum*, *Vaccinium* spp., and *Persea palustris*. In western Louisiana and eastern Texas, baygalls generally occur at stream heads or on short slopes that receive enough seepage to be permanently saturated (Bridges & Orzell 1989; Harcombe *et al.* 1993; Brooks *et al.* 1993; Weakley *et al.* 1998). They are recognized as a natural community in both Louisiana (Louisiana Natural Heritage

Program 1988; Weakley *et al.* 1998) and Texas (Diamond *et al.* 1987; Texas Natural Heritage Program 1993; Weakley *et al.* 1998) and have been described for various localities in the West Gulf Coastal Plain (Watson 1979; Ajilvsgi 1979; Nixon *et al.* 1980; Marks & Harcombe 1981; Nixon *et al.* 1983; Matos & Rudolph 1985; Nixon & Ward 1988; Orzell 1990; Martin & Smith 1991; Brooks *et al.* 1993; Grace & Smith 1995; Van Kley in press).

Interest in an area on the north side of Huntsville State Park (Walker County, Texas), connecting the park to Sam Houston National Forest, alerted us to the presence of a plant community with characteristics similar to a baygall. This community, which occurs along Prairie Branch, is described and discussed in the present paper.

SITE DESCRIPTION

Prairie Branch is fed from the spillway of the lower lake of the man-made Elkins Lake complex and flows directly south on private property through a broad but relatively steep-sided channel for slightly more than 1.4 kilometers before entering the northwest side of Huntsville State Park. The stream is the main source of water for Lake Raven in the park. The flow from Elkins Lake is variable, but a large amount of seepage feeds the stream intermittently along its length on the west side and in scattered areas on the east side.

There are three communities paralleling the stream: bottomland, upland, and "bog" (Figure 1).

Bottomland. Along the creek, mostly about 15 to 50 meters but up to 100 m to either side of it, the alluvium is relatively firm and flat, and the area has physical and vegetative characteristics intermediate between riparian and bottomland communities. The canopy is essentially closed and includes *Nyssa sylvatica*, *Ulmus americana*, *Acer rubrum*, *Liquidambar styraciflua*, *Quercus phellos*, *Fraxinus pennsylvanica*, *Betula nigra*, *Platanus occidentalis*, *Populus deltoides*, *Acer negundo*, and *Salix nigra*. *Carpinus caroliniana* is abundant in the midstory. Characteristic tree species associated with east Texas bottomlands of larger river systems (e.g., *Quercus pagoda*, *Quercus lyrata*, *Carya aquatica*, *Celtis laevigata*, and *Ulmus crassifolia*) are absent along Prairie Branch. The understory is open and few shrubs are present. *Ilex vomitoria* is relatively common but scattered. Characteristic herbaceous species are *Saururus cernuus*, *Hydrocotyle verticillata*, *Poa autumnalis*, *Triadenum walteri*, *Callitriche heterophylla*, *Gratiola virginiana*, *Polygonum hydropiperoides*, *Tovara virginiana*, *Duchesnea indica*, *Chasmanthium latifolium*, *Carex flaccosperma*, *Carex retroflexa*, and *Carex blanda*, and species of *Juncus* and *Rhynchospora*. The ferns *Thelypteris kunthii* and *Onoclea sensibilis* are common near the stream. Two uncommon species are *Hottonia inflata* and *Listera australis*.

Upland. Ridges paralleling Prairie Branch on both its east and west sides rise to about 23 meters above the stream channel. Slopes toward the stream range about 3-8 percent. The ridges and upland margins on both sides of the creek are Alfisols -- sandy above with increasing clay below (McClintock 1979). The slopes bordering and above the bog's edge where the seeps begin are vegetated by a mixed pine-hardwood community typical of the area. The largest and most numerous trees are *Quercus nigra*, with other species mixed in various proportions: *Quercus falcata*, *Nyssa sylvatica*, *Liquidambar styraciflua*, *Ulmus alata*, *Carya texana*, and various individuals apparently intermediate between *Quercus stellata* and *Q. margarettiae*. Most of the larger pines have been removed for timber, but both *Pinus taeda* (more common) and *P. echinata* are found throughout. The most common smaller trees and shrubs are *Cornus florida* and *Sassafras albidum*, mixed with *Morus rubra*, *Viburnum rufidulum*, *Ilex vomitoria*, *Rhamnus caroliniana*, *Ilex opaca*, and *Ilex longipes*. *Carpinus caroliniana* is common along the lower parts of the slope. *Chasmanthium sessiliflorum* is the most common and abundant herbaceous species. *Smilax rotundifolia* is a common vine.

Bog (seepage areas). At the lower slopes of the upland before it flattens out into the stream bottom are a series of linear seepages that parallel the stream. Their slope is 1-3 percent, varying in width from a few dozen meters to perhaps 50 m and extending in places to within 20 m of the stream. On the west side of Prairie Branch they apparently are continuous but are sporadic and reduced in size on the east side. The seeps were flowing and the soil saturated on 18 June 1998, after more than two months of severe drought in the area. The presence of obligate hydrophytes further suggests that seepage occurs all year. The soils are described as Depcor-Huntsburg-Gunter association, which is a combination of Alfisols and Ultisols (McClintock 1979). These wet areas support a dense thicket of low shrubs, bamboo vine *(Smilax laurifolia)*, and taller canopy trees, similar in appearance to tall pocosins (Richardson & Gibbons 1993). Much of the midstory and understory shrubs barely reach a height of 3-5 meters. *Nyssa sylvatica* and *Liquidambar* overtop the shrub layer but do not form a continuous canopy. *Nyssa* is the most common tree species along the upper margins of the seepage areas. Timber has been periodically removed from the uplands and bottomland in the immediate area, but the bog otherwise apparently exists under relatively natural conditions.

Many of the taller trees in the bog are scattered "snags" of individuals (apparently *Nyssa*) that died relatively recently, the cause of death not known but perhaps connected with effects of timber removal along adjacent slopes. Large loblolly pines were recently removed (ca. 1993-1994) from the uplands as well as from along the immediate bog and seep margins, as evidenced by scattered stumps, and this may have affected water flow, increasing seepage and resulting in stress to larger trees.

It is likely that this bog once extended from what is now upper Elkins Lake downstream through Prairie Branch into the bottoms now inundated by Lake Raven in Huntsville State Park. A small remnant of the same bog community exists within the state park at the upper reach of the eastern arm of the lake, near the entrance of Little Chinquapin Creek. The remaining portion of this habitat, along Prairie Branch, is about 25% of what probably was the original bog. The Prairie Branch site is the only known habitat in Walker County similar to a baygall in topography and hydrology. Parts of the next drainage system to the west, which roughly parallels Prairie Branch, are about 15 m higher than Prairie Branch and may significantly contribute to the seepage water. Drainage east of Prairie Branch is lower in elevation.

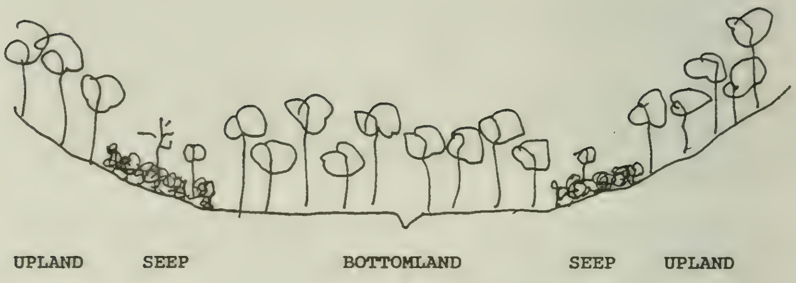

Figure 1. Profile of Prairie Branch.

METHODS

We made several trips to Prairie Branch for observations and collections. On 18 June, 1998, we analyzed five 5 × 5 meter quadrats within the bog. Sites were selected according to accessibility and soil moisture, and ranged from permanently saturated sands to slurry-muck, apparently representing the whole range of moisture conditions. Frequency and diameter of all woody species with a dbh of 2 cm or greater were recorded. Herbaceous species presence was described by identifying all species in the plots; herbaceous cover was measured and percent cover estimated for major species. Percent canopy cover also was estimated. Voucher collections for species are deposited at SHST and TEX. Plant nomenclature follows Jones *et al.* (1997) and Kartesz (1994); scientific authorities for all names used in this paper can be read from these references. A soil sample was collected from the upper 15 cm of each of the five plots and analyzed by A & L Laboratories, Memphis, Tennessee. Organic matter was determined by the combustion method.

RESULTS

Table 1 summarizes the larger woody vegetation in the five plots. *Viburnum nudum* dominated in number of individuals, followed by *Nyssa sylvatica*, *Myrica cerifera*, and *Liquidambar styraciflua*. However, since it never exceeded 3.5 cm dbh, *Viburnum nudum* contributed relatively less to the total basal area than did *Nyssa* or *Liquidambar*. *Smilax laurifolia* was present in large numbers but since the stems were always less than 2 cm diameter, this species is not listed among those in Table 1.

Table 2 summarizes the relative frequency of herbaceous species in the plots. Ten vascular species occurred in all the plots, 6 species in four plots, 8 in three, 9 in two, and 17 in one. A species of liverwort was present in all plots. Fifty vascular and one non-vascular species were identified for the plots during the 18 June survey. About half of these are monocots, with Cyperaceae especially well-represented.

Table 3 gives the percent of herbaceous cover by dominant species in each plot. Only species accounting for 1% or more are included. Cover ranged from 40% to 100%. Monocots and ferns clearly dominated. Canopy cover for the five plots ranged from 20% to 95% but was not correlated with ground cover percentages.

Table 4 gives information on soil samples from the five sample sites. The soils are acidic and low in nutrients and organic matter, falling within the normal range of soil chemistry of baygalls of east Texas and west Louisiana (Hartman 1974; Nixon *et al.* 1980; Nixon & Ward 1988; MacRoberts unpubl.).

DISCUSSION

The seepage areas along Prairie Branch have the physical features and some of the vegetative appearance of baygalls, but most of the typical woody species of baygalls

Table 1. Dominant woody species.

SPECIES	NUMBER OF INDIVIDUALS	TOTAL DIAMETER (cm)	MEAN DIAMETER (cm)	RANGE (cm)
Viburnum nudum	45	105.5	2.3	2.0-3.5
Nyssa sylvatica	23	140.5	6.1	2-20
Myrica cerifera	17	65.0	3.8	2-18
Liquidambar styraciflua	13	111.0	8.5	2-16
Pinus taeda	1	2.0	2.0	2.0
Ulmus rubra	1	3.5	3.5	3.5

Table 2. Species plot occurrence.

SPECIES	OCCURRENCE BY PLOT
Viburnum nudum	12345
Smilax laurifolia	12345
Nyssa sylvatica	12345
Myrica cerifera	12345
Liquidambar styraciflua	12345
Woodwardia areolata	12345
Rhynchospora miliacea	12345
Boehmeria cylindrica	12345
Dichanthelium lindheimeri	12345
Mikania scandens	12345
liverwort	12345
Smilax bona-nox	1234
Hypericum mutilum	1234
Triadenum walteri	1235
Hydrocotyle verticillata	1235
Eleocharis acicularis	1245
Ludwigia palustris	1245
Carex leptalea	123
Chasmanthium laxum	125
Lycopus rubellus	135
Osmunda regalis	245
Eleocharis tortilis	245
Polygonum hydropiperoides	245
Eupatorium compositifolium	245
Juncus effusus	345

Table 2. (cont.).

SPECIES	OCCURRENCE BY PLOT
Osmunda cinnamomea	13
Stachys sp.	23
Quercus nigra	24
Cyperus virens	45
Rhynchospora caduca	45
Rhynchospora corniculata	45
Carex debilis	45
Carex frankii	45
Juncus coriaceus	45
Cyperus thyrsiflorus	1
Acer rubrum	1
Juncus tenuis	1
Ulmus rubra	2
Pinus taeda	2
Micranthemum umbrosum	3
Ptlimnium nuttallii	3
Saururus cernuus	3
Carex lurida	4
Juncus diffusissimus	4
Juncus validus	4
Ludwigia glandulosa	4
Pluchea camphorata	4
Eupatorium perfoliatum	4
Onoclea sensibilis	4
Carex tribuloides	5
Athyrium felix–femina	5

are absent. Conspicuously missing are *Magnolia virginiana* and *Nyssa biflora* (two main components of baygall canopies), *Ilex coriacea, Persea palustris, Persea borbonia, Aronia arbutifolia, Cyrilla racemiflora, Itea virginica, Alnus serrulata*, and others. Instead, a minor baygall species, *Viburnum nudum*, a shrub seldom reaching six meters in height and whose stems are generally only 2-3 cm in diameter, is a major dominant. Also missing are rare, small baygall herbs such as *Burmannia biflora, Apteria aphylla, Mayaca fluviatilis, Habenaria repens, Habenaria clavellata,* and *Pogonia ophioglossoides. Sphagnum,* which can be common in typical baygalls, occurs only in limited quantity along some of the Prairie Branch marginal seeps.

We considered referring to the Prairie Branch bog as a "depauperate" baygall because of its lack of species typical of that community but it is so floristically

Table 3. Percent herbaceous cover.

SPECIES	% COVER
PLOT 1	
Woodwardia areolata	15
Rhynchospora miliacea	10
Chasmanthium laxum	7
Carex leptalea	3
Ludwigia palustris	3
liverwort	2
TOTAL	40%
PLOT 2	
Woodwardia areolata	40
Rhynchospora miliacea	5
Chasmanthium laxum	5
Eleocharis tortilis	3
Ludwigia palustris	3
Polygonum hydropiperoides	2
Triadenum walteri	1
liverwort	1
TOTAL	60%
PLOT 3	
Rhynchospora miliacea	30
Osmunda cinnamomea	20
Woodwardia areolata	15
Carex leptalea	10
Viburnum nudum	10
Boehmeria cylindrica	5
Saururus cernuus	5
Triadenum walteri	3
Dichanthelium lindheimeri	2
TOTAL	100%
PLOT 4	
Chasmanthium laxum	20
Carex frankii	15
Rhynchospora miliacea	15
Juncus coriaceus	10
Carex debilis	5
Dichanthelium lindheimeri	5
Juncus diffusissimus	5
Rhynchospora corniculata	5

Table 3. (cont.).

SPECIES	% COVER
PLOT 4 (cont.)	
Woodwardia areolata	5
Pluchea camphorata	3
Rhynchospora caduca	2
TOTAL	90%
PLOT 5	
Carex frankii	20
Polygonum hydropiperoides	8
Chasmanthium laxum	6
Athyrium felix–femina	5
Rhynchospora miliacea	5
Eleocharis tortilis	3
Osmunda regalis	2
Ludwigia palustris	2
Hydrocotyle verticillata	2
Rhynchospora caduca	2
TOTAL	55%

Table 4. Soil chemistry.

SAMPLE		EXCHANGEABLE IONS (PPM)				
	pH	P	K	Ca	Mg	OM%
Plot 1	5.2	6	36	461	91	2.8
Plot 2	5.0	10	72	782	118	3.9
Plot 3	5.2	12	42	764	133	4.6
Plot 4	4.6	5	26	210	34	1.8
Plot 5	4.7	6	41	517	84	3.7

distinctive that it is misleading to think of it as a baygall. We instead refer to it here as a "possum haw bog."

In San Jacinto County, immediately adjacent to Walker County and less than 50 km (30 miles) southeastward, habitats similar to the Prairie Branch bog are populated by large complements of typical baygall species (Hartman 1974; Nesom pers. observ.; Turner *et al.* in prep.). Brooks *et al.* (1993) studied 20 baygall sites along a north-south axis in eastern Texas. These ran from southern Rusk County south to Hardin and Tyler counties and as far east as Newton County; the closest of these to the Prairie Branch bog was in Tyler County. All are much more similar to the San Jacinto

County baygalls than to the Prairie Branch bog. *Viburnum nudum* was only a minor component at their 20 sites. Clearly, a study similar to that of Brooks *et al.* made along an east-west axis, including western Louisiana, would be valuable.

The possum haw bog and the Big Thicket

The relationship of the floristically depauperate Prairie Branch bog to typical baygalls apparently is analogous to the relationship between the flora of Walker County and that of the southeast Texas Big Thicket. "[The] Baygall-Palmetto Flat complex is considered the heart of the Traditional Thicket and gave this area the name 'Big Thicket' . . . Of all the plant communities of the Big Thicket area, the Acid Bog-Baygall best represents the Traditional Thicket" (Watson 1979). Various authors have included Walker County within the Big Thicket (*e.g.*, Parks & Cory 1936), but using a set of indicator species to define its boundary, McLeod (1971) excluded Walker County from the area. Indeed, a sharp and easily perceptible change occurs near the boundary between San Jacinto County, which has Big Thicket species and vegetation by any definition, and the southeastern corner of Walker County.

Many woody species characteristic of the Big Thicket and the eastern United States drop completely out of the flora in the westward transition into Walker County (Simpson 1988; Burns & Honkala 1990; Nesom 1998; Nesom & Brown in prep.): *Fagus grandifolia, Quercus laurifolia, Pinus palustris, Myrica heterophylla, Magnolia virginiana, Ilex coriacea, Persea palustris, Viburnum acerifolium, Asimina parvifolia, Sebastiania fruticosa, Symplocos tinctoria, Aronia arbutifolia, Clethra alnifolia, Cyrilla racemiflora,* and *Itea virginica.* Among the most characteristic species of moist upland forests in the Big Thicket area of San Jacinto County are the shrubs *Viburnum acerifolium, Asimina parvifolia,* and *Persea borbonia* and the herbaceous *Smilax pumila.* Neither the *Viburnum* nor *Asimina* is known from Walker County, and the latter two species are rare there.

Additionally, a number of other native tree species reach the western boundary of their geographic range within Walker County, where some of them are common before disappearing entirely only a few more miles to the west: *Liquidambar styraciflua, Acer rubrum, Quercus velutina, Quercus alba, Carpinus caroliniana, Ostrya virginiana, Sassafras albidum,* and *Chionanthus virginicus. Magnolia grandiflora, Carya myristiciformis, Quercus michauxii, Hamamelis virginiana, Castanea pumila, Styrax americana, Halesia diptera,* and *Rhododendron canescens* are rare in Walker County, their last outpost westward. Other tree species are very near their western distributional boundary in Walker County (for example): *Pinus echinata, Pinus taeda, Cornus florida, Nyssa sylvatica, Diospyros virginiana, Carya cordiformis, Carya aquatica, Betula nigra, Quercus falcata, Quercus phellos,* and *Quercus lyrata.*

The predominance of clay soils in western Walker County and further west is surely connected with this abrupt limitation of species distributions, but other limiting environmental factors are not so clear or sharply defined. Braun (1950), however, noted that "decreasing precipitation and longer and more frequent droughts" were the primary limitations to westward spread of the deciduous forest, and it seems likely that the prolonged, high seasonal temperatures in southeast Texas have a strong effect in limiting the water available to plants. The annual average 112 cm/44 in of precipitation in Huntsville/Walker County (Larkin & Bomar 1983), rapidly depleted by the prolonged heat, probably approaches the minimal amount required by many woody species of this area. Rainfall increases quickly eastward from Huntsville (ca. 117 cm/46 in -- Coldspring/San Jacinto County [40 km eastward]; 122 cm/48 in -- Livingston/Polk County [60 km eastward]; 132 cm/52 in -- Jasper/Jasper County [150 km eastward) and decreases to the west (99 cm/39 in -- College Station/Brazos County [80 km westward]; 91 cm/36 in -- Bastrop/ Bastrop County [160 km westward]; 81 cm/32 in -- Austin/Travis County [210 km westward]).

Along Prairie Branch, why should only *Viburnum nudum* occur, one of many shrubby, characteristic baygall species that appear to be strictly true to this constantly wet stream bottom habitat? Perhaps plants of possum haw are more tolerant to occasional drought, but then the species might be expected to occur in a broader range of habitats, which it does not. Possum haw and bamboo vine have reached Prairie Branch relatively recently through dispersal from baygalls in more eastern sites, or the Prairie Branch site may be floristically depleted from earlier, more typical, western baygalls.

A possum haw bog in Anderson County

We report here another east Texas bog that is floristically and physically similar to the Prairie Branch site. On July 30, 1998, the two MacRoberts examined a "baygall" at the western end of Andrew's Bog in the Engeling Wildlife Management Area, Anderson County, about 150 kilometers north of Prairie Branch in the Post Oak Savanna region of Texas. Like the Prairie Branch site, Andrew's Bog is at the edge of the Eastern Deciduous Forest.

The midstory and overstory were dominated by *Viburnum nudum*, *Nyssa sylvatica*, *Myrica cerifera*, and *Liquidambar styraciflua*, with scattered individuals of *Acer rubrum*. As at Prairie Branch, the Andrew's Bog site had no *Magnolia, Persea*, or *Ilex coriacea*; neither was there any *Smilax laurifolia*, although there was a small amount of *Smilax bona-nox*. The ground cover was somewhat different from that at Prairie Branch. Ferns dominated, notably *Woodwardia areolata* and *Osmunda cinnamomea*, with some *Osmunda regalis*. *Sphagnum* and liverworts were common. Other species present were *Chasmanthium laxum, Saururus cernuus*, *Athyrium felix-femina*, *Eleocharis* spp., *Rhynchospora* spp., and *Carex* spp., the latter two genera in fewer species and in fewer numbers than at Prairie Branch. As at Prairie Branch, none of the rare, small baygall herbs mentioned above were present.

The Andrew's Bog site is at the lower slope of a deep sand hill, topographically similar to Prairie Branch. The Andrew's Bog soils also were similar to those at Prairie Branch – deep wet muck – even though the area was in severe drought.

The environmental variables of biological importance in this region at the very edge of the Eastern Forest have not been fully explored (Owen & Schmidly 1986), and many interesting possibilities exist for studying the plant ecology in this area of sharp transition. Bog sites are scattered westward in Texas as far as the eastern edge of the Edwards Plateau, and characterization of these may provide insight into the nature and origin of the communities in Walker County and Andrews County. We hope that at least representative natural communities will remain intact enough to allow this.

ACKNOWLEDGMENTS

We thank Larry Brown (Houston Community College), Jim Neal (Texas Parks & Wildlife Department), and David Riskind (Texas Parks & Wildlife Department) for their comments and observations on the manuscript.

LITERATURE

Ajilvsgi, G. 1979. *Wild Flowers of the Big Thicket*. Texas A&M Univ. Press, College Station, Texas.

Braun, E.L. 1950. *Deciduous Forests of Eastern North America*. Hafner Publ. Co. (reprint 1964, 1967), New York, New York.

Bridges, E.L. & S.L. Orzell. 1989. Longleaf pine communities of the west gulf coastal plain. Natural Areas J. 19:246-263.

Brooks, A.R., E.S. Nixon, & J.A. Neal. 1993. Woody vegetation of wet creek bottom communities in eastern Texas. Castanea 58:185-196.

Burns, R.M. & B.H. Honkala (technical coords.). 1990. *Silvics of North America*. Vol. 1, *Conifers*; Vol. 2, *Hardwoods*. Agriculture Handbook 654. U.S.D.A., Forest Service, Washington, D.C.

Christensen, N.L. 1988. Vegetation of the southeastern Coastal Plain. Pp. 317-363, *in* Barbour, M.G. & W.D. Billings (eds.), *North American Terrestrial Vegetation*. Cambridge Univ. Press, New York, New York.

Diamond, D.D., D.H. Riskind, & S.L. Orzell. 1987. A framework for plant community classification and conservation in Texas. Texas J. Sci. 39:203-221.

Grace, S.L. & L.M. Smith. 1995. A survey and description of the natural plant communities of the Kisatchie National Forest, Vernon District. Unpubl. report, Louisiana Dept. of Wildlife and Fisheries, Baton Rouge, Louisiana.

Harcombe, P.A., J.S. Glitzenstein, R.G. Knox, S.L. Orzell, & E.L. Bridges. 1993. Vegetation of the longleaf pine region of the west Gulf coastal plain. Proc. Tall Timbers Fire Ecology Conference 18:83-104.

Harper, R.M. 1914. The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession. Bull. Torrey Bot. Club 41:209-220.

Hartman, D.H. 1974. Forest structure of the Big Thicket Scenic Area, Texas. M.S. Thesis, Texas A & M University, College Station, Texas.

Jones, S.D., J.K. Wipff, & P.M. Montgomery. 1997. *Vascular Plants of Texas*. Univ. Texas Press, Austin, Texas.

Kartesz, J.T. 1994. *A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland*. Timber Press, Portland, Oregon.

Larkin, T.J. & G.W. Bomar. 1983. *Climatic Atlas of Texas*. Univ. Texas Press, Austin, Texas.

Louisiana Natural Heritage Program. 1988. The natural communities of Louisiana. Unpubl. report, Louisiana Dept. of Wildlife and Fisheries, Baton Rouge, Louisiana.

McLeod, C.A. 1971. The Big Thicket forest of East Texas. Texas J. Sci. 23:221-233.

McClintock, W.R., Jr., J.J. Castillo, & M. Stewart. 1979. *Soil Survey of Walker County, Texas*. U.S.D.A. Soil Conservation Service.

Marks, P.L. & P.A. Harcombe. 1981. Forest vegetation of the Big Thicket, southeast Texas. Ecol. Monogr. 51:287-305.

Martin, D.L. & L.M. Smith. 1991. A survey and description of the natural plant communities of Kisatchie National Forest, Winn and Kisatchie Districts. Unpubl. report, Louisiana Dept. of Wildlife and Fisheries, Baton Rouge, Louisiana.

Matos, J.A. & D.C. Rudolph. 1985. The vegetation of the Roy E. Larsen Sandylands Sanctuary in the Big Thicket of Texas. Castanea 50:228-249.

Nesom, G.L. 1998. *Trees of Huntsville and Walker County, Texas, & Big Tree Register.* Sam Houston Press, Sam Houston State University, Huntsville, Texas.

Nesom, G.L. & L.E. Brown. In prep. Annotated checklist of the vascular plants of Walker, Montgomery, and San Jacinto counties, Texas.

Nixon, E.S., J.W. Higgins, P.L. Blanchette, & F.A. Roth. 1980. Woody vegetation of a wet creek branch in east Texas. Texas J. Sci. 32:337-341.

Nixon, E.S., R.L. Ehrhart, S.A. Jasper, J.S. Neck, & J.R. Ward. 1983. Woody, streamside vegetation of Prairie Creek in east Texas. Texas J. Sci. 35:205-213.

Nixon, E.S. & J.R. Ward. 1988. Vegetation of a wet creek bottom site in eastern Texas. Texas J. Sci. 40:358-361.

Orzell, S.L. 1990. *Texas Natural Heritage Program Inventory of National Forests and National Grasslands in Texas.* Unpubl. report (to the U.S. Forest Service, Lufkin TX), Texas Natural Heritage Program, Austin, Texas.

Owen, J.G. & D.J. Schmidly. 1986. Environmental variables of biological importance in east Texas. Texas J. Sci. 38:99-117.

Parks, H.B., V.L. Cory, *et al.* 1936. Biological survey of the East Texas Big Thicket area: The fauna and flora of the Big Thicket area. Sponsored by the Texas Academy of Science.

Richardson, C.J. & J.W. Gibbons. 1993. Pocosins, Carolina bays, and mountain bogs. Pp. 257-310, *in* W.H. Martin, S.G. Boyce, & A.C. Echternacht (eds.), *Biodiversity of the Southeastern United States. Lowland Terrestrial Communities.* Wiley, New York, New York.

Simpson, B.J. 1988. *A Field Guide to Texas Trees.* Texas Monthly Press, Austin, Texas.

Texas Natural Heritage Program. 1993. *Plant Communities of Texas* (series level). Unpubl. report; data now maintained by Texas Parks & Wildlife Department, Austin, Texas.

Turner, R.L., J.E. VanKley, & L.S. Smith. In prep. *Field Guide: Ecological Classification System for the National Forests and Adjacent Areas of the West Gulf Coastal Plain.* The Nature Conservancy.

Van Kley, J.E. In press. The vegetation of the Kisatchie sandstone hills, Louisiana. Castanea.

Watson, G. 1979. *Big Thicket Plant Ecology: An Introduction* (ed. 2). Big Thicket Museum Publication Series, No. 5. Big Thicket Museum, Saratoga, Texas.

Watson, G. 1982. *Vegetational Survey of Big Thicket National Preserve.* Unpubl. report submitted to the Big Thicket National Preserve, Beaumont, Texas.

Weakley, A.S., K.D. Patterson, S. Landall, M. Pyne, & others (compilers). 1998. *International classification of ecological communities: Terrestrial vegetation of the Southeastern United States.* Working draft, The Nature Conservancy, Southeast Regional Office, Chapel Hill, North Carolina.

Wells, B.W. & I.V. Shunk. 1928. A southern upland grass-sedge bog: an ecological study. Technical Bull. 32, North Carolina Experimental Station, Raleigh, North Carolina.

Phytologia (November 1997) 83(5):384.

NEW NAMES IN THIS ISSUE OF PHYTOLOGIA

As a result of the International Botanical Congress in Tokyo in 1993, the International Association of Plant Taxonomy has been tasked with exploring the feasibility of registration of plant and fungi names. In accordance with terms of the pilot implementation of the registration concept, new names and combinations produced in this issue of PHYTOLOGIA are listed below.

New name or combination	Page Number
Elymus stebbinsii Gould subsp. ***septentrionalis*** Barkworth, *subsp. nov.*	360

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